INFANT SOCIALISATION IN OLIVE BABOONS *(Papio anubis)*

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I, Suzanne Mary Harvey, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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ABSTRACT

Baboons live in social groups and environments that are similar to early hominids, thus they provide a good model for the study of the evolution of human behaviour. Adult baboons (*Papio anubis*) exhibit complex social behaviour and communication skills, but the process by which they acquire these behaviours has not previously been investigated. Understanding infant socialisation – the process of development from complete maternal dependence to an independent member of a social group – provides insight into the evolution of human behaviour and language.

Audio recordings and behavioural data were collected from olive baboons in Gashaka Gumti national Park, Nigeria. This is a marginal environment, with temperatures and rainfall more extreme than other baboon study sites. Physical interactions with the mother (e.g. weaning, being carried), physical interactions with other group members (being taken from mother; 'infant handling'), and vocal communication are documented from birth to weaning.

Infant socialisation in Nigerian baboons is characterised by frequent aggressive and affilitative handling by adults in the first 6 months of life, and a limited vocal repertoire of which three calls are produced from birth, and one is produced after 7 months of age. Only one call shows evidence of context specificity, and communication most likely takes place in the form of an online readout of an infant's emotional state.

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SECTION I:

INTRODUCTION

CHAPTER 1:

INTRODUCTION

Infant male Eggi with his mother, Rabi, on the day of his birth. Photo: Suzanne Harvey, 2011.

INTRODUCTION

The nature of the intellectual and cognitive abilities possessed by humans and other animals has been the subject of debate for many centuries. Historically, the focus of this debate emphasised differences between humans and other species; from the Aristotelian distinction between 'human rationality' and 'animal instinct', to the Cartesian distinction between 'mechanistic animals' and 'intellectual humans' (Ogle 1943; Hatfield 2008). One way to learn about the origins of human cognitive abilities is via the comparative method, i.e. the study of cognitive abilities in other species. Following the publication of the *On the Origin of Species* in 1859, the more other species are studied, the more such distinctions appear obsolete, "it is a significant fact, that the more the habits of any particular animal are studied by a naturalist, the more he attributes to reason, and the less to unlearnt instinct" (Darwin 1871, Book I, p.46). While theories of animals as mechanistic and reflex-driven focus on their reactions to environmental challenges, the *social brain hypothesis* (Dunbar 1998) proposes that the evolution of cognition is driven by the social challenges resulting from living in large or complex groups; therefore species with similar social structures would be expected to possess similar cognitive traits. Thus, from the study of other group living primate species, it is possible to infer how such cognitive traits evolved, and which social pressures favour advanced cognitive abilities.

Social behaviour, language and tool use are often cited as the three areas according to which human and non-human primates can be divided (Gibson 1994), with human achievements in these areas being qualitatively greater than those of other primates. These three behaviours are linked to underlying

cognitive abilities that allow behavioural flexibility observational learning (van Schaik et al. 1999), and therefore it has become common practice for researchers to seek such 'benchmarks' of human evolution. In the case of tool use, this behaviour was once thought to be uniquely human, but there is now much evidence of complex tool use in non-human ape species (hereafter referred to as apes), particularly chimpanzees. There is even evidence of socially driven differences in tool use between geographically isolated groups of the chimpanzees (Fowler and Sommer 2007). Thus, the binary 'can/cannot' distinction with regard to tool use is now less clear. Baboons are far less proficient in tool use than chimpanzees (Beck, 1974) but complex social interactions and language can be investigated in this species. By documenting social behaviour and vocal communication from birth to weaning in olive baboons, the current study aims to elucidate the evolution of the human cognitive abilities that enable sophisticated social interaction and complex language.

Why Study Baboons?

The typical models for human evolution tend to be based on phylogenetically close species such as chimpanzees (*Pan troglodytes*; Susman 1986) or species adapted to ecologically similar conditions to early hominids, such as baboons (Strum and Mitchell 1986). Olive baboons (*Papio anubis*), like chimpanzees, live in large, multi-male, multi-female groups, in which understanding of complex triadic social interactions would be highly beneficial. The social structure of baboon groups is also analogous to those of early hominids, making them ideal for studying human evolution (Strum and Mitchell 1986). They have been shown to understand complex social interactions (e.g.

Crockford et al. 2007), and display behavioural and vocal flexibility (Cheney and Seyfarth 2007; Ey et al. 2007; chapter 2). To date, it is not known whether these abilities are largely innate, or whether behavioural and vocal flexibility develops throughout infancy via socialisation, in the same way that social understanding develops in humans after the first few years of life (Piaget 1952).

In addition to the social similarities that make baboons a suitable model for early hominids, they can also range in forest and savannah habitats, creating similar environmental conditions. Moreover, baboons have long held a particular fascination when it comes to language and communication, prompting Charles Darwin to state that “He who understands baboon would do more towards metaphysics than Locke” (Darwin, M Notebook, 1838).

From Jan-Apr 2010, the author carried out a pilot study into the behaviour of olive baboons in the Gashaka Gumti National Park in Nigeria, as part of the Gashaka Primate Project. The present study documents infant socialisation in a group of baboons that range in both forest and savannah habitats within the national park. This is a marginal habitat for baboons (chapter 2), therefore it is also possible to draw implications about the effects of environment on infant development by comparing the study group to other populations (chapter 3).

Background

Infant socialisation

Having chosen to focus on infant socialisation to assess the development of complex social abilities in primates, key behaviours that reflect social

development must be identified. For this, three main dimensions of an infant's socialisation have been selected – (a) physical interaction with its mother, (b) physical interaction with individuals other than its mother, and (c) communication via vocalisations during all interactions. In accordance with these overarching themes, data have been collected to investigate: (a) infant activity budgets from birth to weaning, (b) handling of infants by other adults, (c) the infant vocal repertoire, and (d) context specificity of vocalisations. These data form the 4 data chapters of the current study, together describing the characteristics of infant socialisation in olive baboons.

In its simplest form, infant socialisation describes how an individual develops from an infant that is dependent on its mother, to an independent individual that is part of the complex social structure of a group. For this reason, activity budgets from birth to weaning are compared to adult activity budgets (chapter 3) to assess general differences. Since the field site is a marginal environment, infant activity of the study group is also compared to that of infant baboons at other study sites. Activity budgets reveal the changing nature of interactions between mother and infant as the infant ages, such as a reduction in the time spent nursing. These basic changes in behaviour form the basis of further analyses of infant interaction with adults other than their mother, via infant handling (chapter 4), and infant communication in a range of contexts (chapters 5 and 6).

Infant Handling and the Market Value Theory

Since the overall aim of investigating infant socialisation is to understand how infants develop into fully functioning members of a social group, one theory of

infant handling is of particular interest – the Market Value Theory (Henzi and Barrett 2002). Theories of infant handling are reviewed in detail in chapter 4, and therefore here, its importance to the study of socialisation is discussed. While all theories of infant handling tend to focus on the interaction between mother and handler (14 theories reviewed in Maestripieri 2011; detail chapter 4), the Market Value Theory is distinguished by its use of tradable commodities. Thus, the infant is seen as a passive commodity that the mother and handler can trade. If this is the case, then how do infants develop from a passive, tradable commodity to an individual group member that has a full role in social interactions with others? In other words, how do infant handling interactions affect the ontogeny of socialisation?

By disrupting the mother-infant relationship in captivity, early social experiences have been shown to have significant affects on aggressive and submissive behaviours in macaques (Coelho and Bramblett 1981) with peer-raised infants displaying less of both behaviours than mother-raised infants. Additionally, peer-raised infants displayed more affiliative behaviours such as social approaches and holding other individuals than mother-reared infants (Coelho and Bramblett 1984). Thus, early social experiences, in the case of these studies 0-12 weeks, can have a significant effect on the ontogeny of socialisation. Most infant handling interactions take place during this 0-12 week period, and some studies focus only on handling of infants of this age (e.g. Henzi and Barrett 2002). In terms of infant handling, there have been observations of both positive (Schino et al. 2003) and negative effects (Kleindorfer and Wasser 2004) on infants (reviewed in chapter 4). The worst case scenario for the infant is an increased mortality rate associated with

negative infant handling (Kleindorfer and Wasser 2004), therefore it is expected that when infants are very young, mothers will resist aggressive handling. As they become more independent, infants should resist aggressive handling themselves.

One aim of the current study is to document the transition from a passive commodity to an independent individual via socialisation. Market Value Theory is based on data from infants aged 0-3 months. To investigate all characteristics of infant handling (Chapter 4), firstly Henzi and Barrett's study is replicated, to determine whether there is a market for infants in the current study group. Analyses are then extended to include all unweaned infants up to 21 months of age to assess changes in the handling of infants as they mature.

Communication

Many aspects of language have been cited as uniquely human, such as sentence structure and grammar (Chomsky 1959). Noam Chomsky, the most prominent proponent of language as an exclusively human phenomenon (e.g. Chomsky 1959) argues that no other animal could acquire language in the spontaneous way that humans do. Early studies of primate communication tend to support this absence of grammar and syntax, as well as limitations in learning.

The classic 'ape language studies' are a group of studies that focus on the extent to which great apes can communicate using verbal or signed human language. An early documentation of the language differences between chimpanzees and humans came from the chimpanzee Gua, who was raised alongside a human child to assess their developmental differences (Kellogg

and Kellogg 1933). While the human infant began to use words naturally, Gua failed to acquire any words at all. Following this experiment, one of the first ape language studies to focus on training an infant chimpanzee, Viki, to produce words in English (Hayes and Hayes 1952) was also largely unsuccessful. Despite trainers physically manipulating her mouth in an attempt to aid in the formation of words, Viki was only able to produce 4 words, which were simple (mama, papa, up, cup) and were not spoken clearly.

While verbal language training has had very limited success, chimpanzees trained to use American Sign Language (ASL) have demonstrated far greater communication abilities. In the first few months of training, chimpanzees Washoe (Gardner and Gardner 1969) and Nim Chimsky (Terrace 1979) learnt 34 and 125 signs respectively, and both were able to combine them to make new meanings. Nim Chimsky eventually produced 19,000 combinations, but despite this large degree of flexibility, sign combinations lacked any grammar or rule structure. The gorilla Koko (*Gorilla gorilla gorilla*) learnt approximately 2000 signs (Patterson 1978) and was able to communicate emotional concepts such as ‘sad’, but again lacked sentence structure or grammar in her sign combinations.

Arguably the most successful ape language study was that of Kanzi, a male bonobo (*Pan paniscus*), who learnt to communicate through a lexigram board. The symbols on this board generated the words they represented, creating a verbal ‘conversation’ between Kanzi and his trainers. Using this equipment, Kanzi was able to answer a series of 416 complex questions with a 74% success rate, far exceeding the communication abilities of ASL trained apes.

While for humans, much communication takes place vocally, the ape language studies suggest that in other apes, understanding of communication far exceeds vocal ability. An inability to manipulate the mouth and tongue, as well as a vocal tract that cannot close entirely, have been cited as reasons for the limited vocal ability of non-human primates (e.g. Falk 1975). This has a genetic basis in the FOXP2 gene, in which mutations in humans lead to similar impairments in speech production (Liegois et al. 2002).

Besides the limited success in terms of word acquisition, another issue with the use of language training in the study of ape communication is that it has very little ecological validity. Vocalisations produced in the natural environment of a study species allows one to investigate the function of such vocalisations in a way that language training cannot. Therefore, the paradigm has now moved on from teaching language to non-human primates, and focuses on communication in the natural environment. This approach is important in terms of the evolution of language and in particular the current study, since baboons have been chosen as a study species due to their similar ecological conditions to early hominids (Strum and Mitchell 1986). Thus, to infer anything about human evolution from the study of baboon behaviour, use of communication in the natural environment is key.

Adult baboons have been shown to respond differently to different variants of calls (Fischer et al. 2001), therefore this ability must either be present at birth, or develop during infancy. Since no previous studies have described the infant olive baboon vocal repertoire, the acoustic parameters that define calls are described in the current study, and these calls are grouped into various call types according to their acoustic features (chapter 5). Numerous primate

studies have demonstrated the use of calls with specific meanings (vervet monkeys: Seyfarth et al. 1980) as well as call affixation, (Campbell's monkeys: Ouattara et al. 2009) combination (chimpanzees: Crockford et al. 2005) and (bonobos: Clay and Zuberbuehler 2011to generate flexible communication (chapter 6). Thus, in addition to defining the vocal repertoire, vocalisations are analysed at the levels of individual calls, call combinations and call sequences, all with reference to the contexts in which they are produced.

Objectives

To begin investigating how baboons develop the complex social behaviour that characterises their adult behaviour, this study has the following specific aims:

- To explore the changes in activity budgets in olive baboons, from birth to weaning. To compare infant behaviour with adult behaviour at the same study site, and compare this behaviour to other study populations, to assess environmental effects on infant behaviour (chapter 3).
- To investigate the function of infant handling in olive baboons, specifically evaluating the Market Value Theory, and describing the changing characteristics of handling as infants age (chapter 4).
- To define the vocal repertoire of infant baboons from birth to weaning, using acoustic features to categorise different call types (chapter 5).
- To assess whether specific vocalisations are produced in different contexts, and explore how the functional referentiality of the adult vocal repertoire is developed as infants age (chapter 6).

SECTION II:

THE BABOONS OF GASHAKA

CHAPTER 2:

GENERAL MATERIALS AND METHODS

Suzanne Harvey, Georgia Patey and Ibrahim Usman (L-R) with baboons near Kwano field station during data collection. Photo: Nicole Thompson, 2011.

STUDY SITE

The Gashaka Primate Project

Studies of baboon infant socialisation form part of the long-term conservation and research efforts of the Gashaka Primate Project (GPP; www.ucl.ac.uk/gashaka; Sommer and Ross 2011). GPP's Kwano field station, where the baboon study group has its home range, is situated near the village of Gashaka, in Nigeria's Gashaka Gumti National Park. This reserve is located in southern Taraba State, eastern Nigeria, along the border with Cameroon (06° 55' – 08° 13' N and 11° 13' N – 12° 11' E; Fig. 02.01). Created by the merging of two game reserves in 1991, Gashaka Gumti is Nigeria's largest national park at 6,731 sq km (Dunn 1999, Chapman and Chapman 2001, Chapman et al. 2001).

Fig. 02.01. Location of Gashaka Gumti National Park (A). Image: Google Maps, 2013.

GPP was founded in the year 2000 by Volker Sommer (VS) and has since become part of an international network of researchers that currently includes institutions in over a dozen countries (Federal University of Technology Yola / Nigeria, Gombe State University / Nigeria, Universität Frankfurt / Germany, Universität Würzburg / Germany, University of Alabama at Birmingham / USA, University of Canterbury / New Zealand, University of Chicago / USA, University of Copenhagen / Denmark, University of St. Andrews / UK, Academy of Sciences of the Czech Republic Bron / Czech Republic, Deutsches Primatenzentrum at Göttingen / Germany, International Institut for Tropical Agriculture at Ibadan / Nigeria, Leibniz-Institut für Zoo- und Wildtierforschung at Berlin / Germany, Max-Planck-Institut für Evolutionäre Anthropology at Leipzig / Germany). In addition to its research activities, the project is also linked to various conservation organisations (North of England Zoological Society / Chester Zoo, Wildlife Conservation Society, Great Ape Programme of the US Fish and Wildlife Service, Nigerian Conservation Foundation, WWF-UK). Core funding for the maintenance of field facilities is provided by the Nigeria Biodiversity Programme of the North of England Zoological Society / Chester Zoo (Pascual-Garrido 2012).

Fig. 02.02. Kwano field station in dry season, with living quarters to the right, the office to the rear, and the 'power-island' hybrid facility to the left (photograph: Suzanne Harvey, 2010).

The GPP infrastructure comprises two main study sites, with a five room research station at Gashaka village on the outskirts of Gashaka Gumti National Park, and a 16 room field station at Kwano, the site of an abandoned village of the same name (Fig. 02.02). There are habituated baboon groups at both sites, though the current study into infant socialisation took place exclusively at Kwano field station. Kwano lies approximately 11 aerial km from Gashaka village (583 m above sea level; 07° 19' N – 11° 35' E). The two sites are linked by an ancient footpath that continues into the highlands of Nigeria and on to Cameroon, though this route is only suitable for travelling on foot or

by motorcycle for most of the year. Communication is restricted to walkie-talkies within the national park, and satellite phones are needed for communication further afield. Since 2005, power has been supplied to Kwano all year round via a hybrid system of photovoltaic energy generated by solar panels located at the field station, and hydroelectricity generated from a nearby waterfall. This system is referred to as the ‘power-island’ (cf. Fig. 02.02).

GPP employs a permanent staff of approximately a dozen local field assistants, whose roles range from accompanying researchers in the field, to independent data collection. Basic data collected by both field assistants and researchers provides long term information on environmental variables such as temperature, rainfall and phenology, as well as data on the changing demography and basic behavioural patterns of the baboon study groups. These long term data sets are available to researchers to use alongside their own data. While initially the research carried out in association with GPP was restricted to ecological and behavioural studies of non-human primates, it now hosts a range of projects. These reflect the high level of biodiversity in the area, from insects and amphibians to birds and mammals, and also include studies into the geography and phenology of Gashaka Gumti National Park. The current study into infant socialisation in baboons is part of this move towards interdisciplinarity, falling into categories such as behaviour, cognition, developmental psychology and vocal communication research.

Habitat and Climate

Gashaka Gumti National Park located in the sub-Saharan Guinea Savannah zone, and is divided into two sectors. Gumti, named after a village in the north of the reserve, is a mainly flat biome consisting of grass and trees. This savannah environment is home to large mammals such as lions and elephants, which are not present in the southern, Gashaka sector. The Gashaka sector consists of lowland (< 825 m), sub-montane, and montane (> 1650 m) strata, creating a mosaic of savannah, woodland, riverine, grassland and lowland rainforest habitats with Kwano field station lying within the forest-grassland transition zone (Fig. 02.03). Within the home range of the Kwano study group, the habitat has been recorded as approximately 65% lowland and gallery rainforest, and 35% guinea savannah woodland (Higham et al. 2006). As the field station occupies the site of a former village, three areas consist of former tree crops, and are denoted oil palm forest and mango forest (Warren 2003). In contrast to the flat Gumti region, terrain in the southern Gashaka sector includes steep hills, and altitudes range from 300-2,400 m. There are many rivers, which flow all year round, despite a distinct dry season from Nov – Apr, during which very little rain falls. Often there is no rain at all during this time, and winds carrying dust from the Sahara, known as the Harmattan, sometimes occur during dry season. From mid Apr to mid Nov, there is regular heavy rainfall.

Fig. 02.03. Forest (top) and grassland (bottom) habitats in the Kwano area of Gashaka Gumti National Park (photos: Suzanne Harvey, 2010; Georgia Patey, 2011).

The pronounced seasonal differences in rainfall correspond with significant temperature fluctuations. Data collected from 2001-2008 as part of long term data collection at Kwano revealed differences in both average temperatures and the range of temperatures between the four wettest months (°C: Dec 18–31, Jan 17–30, Feb 20–34, Mar 22–36; average 13.5 degrees difference) and four driest months (°C: Jun 22–31, Jul 22–30, Aug 22–31, Sep 22–31; average 8.8 degrees difference (Sommer and Ross 2011). The mean minimum temperature was 20.9 °C, and the mean maximum 32.2 °C, though extremes of 12 °C and 43 °C have been recorded.

During this time period, 38% of days were classed as rainy days per month, and there was an average of 146 days with rain per annum. Average annual rainfall at Kwano was 1,935 mm, ranging from 1,638-2,337 mm. The highest rainfall recorded was 125 mm, with such heavy rain usually falling in September.

STUDY ANIMALS

Baboons are Old World primates of the *Papio* genus, and the cercopithecine subfamily. Traditionally, five different subspecies of baboon are distinguished – olive (*P. Anubis*), yellow (*P. cynocephalus*), Guinea (*P. papio*), chacma (*P. ursinus*), and hamadryas (*P. hamadryas*). However, some authors categorise all species as subspecies of hamadryas baboons (e.g. Jolly 1993). Certainly, there is much debate surrounding the classification of baboons. Generally, olive baboons are found in south, central and east Africa, yellow baboons in south-central and eastern Africa, Guinea baboons in the far west, chacma baboons in southern Africa, and hamadryas baboons across south Africa and southwest Arabia (Newman et al. 2004). However, while these different

subspecies have separate geographical distributions (Jolly 1993), there is much overlap and some interbreeding, including that of olive and yellow baboons (Alberts et al. 2001). A recent genetic study (Zinner et al. 2009) was unable to reliably distinguish between the five subspecies, and found within and between group differences in the mitochondrial DNA of baboons from 53 study sites, spanning their entire range across Africa (Fig. 02.04). This suggests multiple periods of isolation and rejoining in the evolutionary history of baboons. The different species often have different appearances and social behaviour, with hamadryas baboons living in harem groups with one male and many females (Kummer 1968) and others, including olive baboons, living in multi-male groups.

It has been pointed out that using different baboon species interchangeably in biomedical research is not reliable due such genetic differences (Williams-Blangero et al. 1990) and with differing social structures, it is highly likely that behavioural differences between species and populations will also be present.

Olive baboons (Fig. 02.05) are the most widespread of the baboon species, and their conservation status is classified as ‘least concern’ by the IUCN red list. They live in large, multi-male, multi-female social groups (Dunbar and Dunbar 1974), with male dispersal and female philopatry (Smuts 1985). Males emigrate to neighbouring groups when adult (Smuts 1985), and infanticide has been observed during immigration of new males (Smuts 1985, Palombit 2003). Males compete for access to fertile females, and sexual consortships and mate guarding are common (Berkovitch 1983). Social organisation is

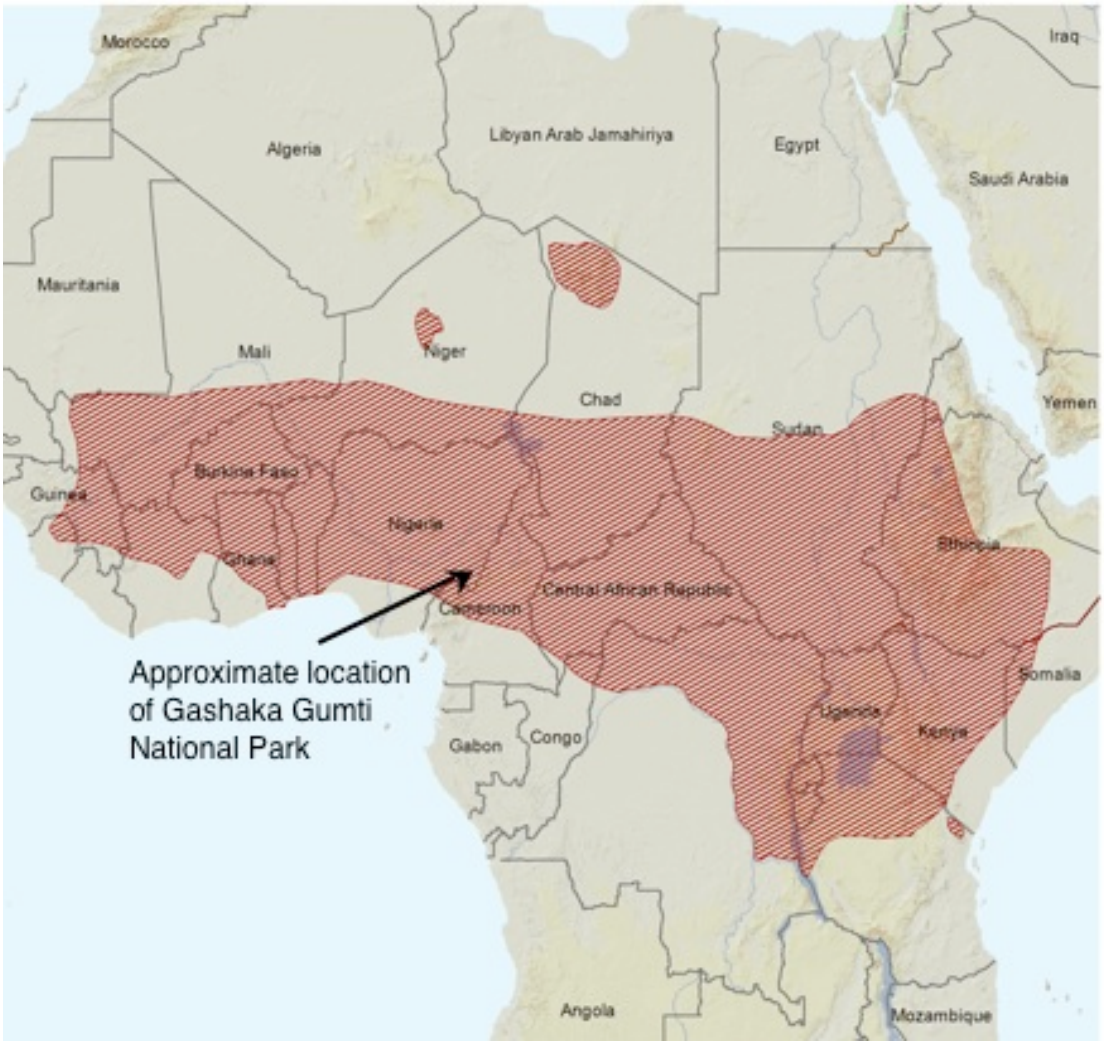

Fig. 02.04. Distribution map of olive baboons; hatched areas show where baboons are present. The Gashaka Gumti National Park lies on the southern edge of their western range. Image: adapted from IUCN red list.

characterised by a linear dominance hierarchy (Smuts 1985). There is no seasonality in breeding, and gestation lasts for approximately 6 months (Berkovitch and Harding 1993). At birth, infants have a black natal coat (Fig. 02.06), which gradually transitions into the pale brown adult coat from approximately 5 months of age (Ransom and Rowell 1972; Fig. 02.07). Although they then appear similar to juveniles, this change in appearance does

not coincide with weaning, which has been recorded as between 8-10 months (Nash 1978; for weaning detail, see chapter 3). While generally accepted, this description is based on study groups in central and east Africa, with little known about West African populations.

Kwano Baboons

Kwano is an unusual study site for olive baboons, and is at the edge of the range of their taxon across Africa, with the majority of baboon study sites being within the savannah zone (cf. Fig. 02.04). Thus, most studies of olive baboons are from open habitats, with little known about groups such as Kwano Troop that occupy closed canopy forests. Compared to 14 established baboon study sites, Kwano is also an extreme outlier in terms of rainfall and temperature, with the average annual rainfall for 2001-2006 (2022 mm) and average temperature (26.4 ℃) being significantly higher than those of all other comparison sites (Higham et al. 2006). Baboons are a large, heavy primate that must compete with other species at this site that are better adapted to the forest environment, such as colobus, mona and putty nose monkeys, and chimpanzees. The mean troop size of baboons at GGNP is significantly lower than that of 14 other censused, non-GGNP baboon groups, with the Kwano average being 22.3 (Ross et al. 2009). Their home range size is average for baboons, at 2.4 km, (Warren 2003).

Fig. 02.05. Infant and juvenile olive baboons at Gashaka Gumti National Park. Photograph: Suzanne Harvey, 2010.

Fig. 02.06. Infant baboon approximately 2 weeks old at Gashaka Gumti National Park, showing the black natal coat which is lost at around 5 months of age. Photograph: Rebecca Boulton, 2011.

Fig. 02.07. Infant baboon aged approximately 5 months old at Gashaka Gumti National Park, showing the transition between natal and adult colouring. Photograph: Rebecca Boulton, 2011.

Cases of leopards preying upon baboons have been documented at other sites (Altmann 1980) and leopards were present in the Kwano area during data collection. Thus, they are a potential threat to the study group. However, predation risk is assumed to be low, as no healthy individuals disappeared during data collection.

Eleven different plant parts have been identified as those consumed by baboons in Gashaka Gumti National Par: flower bracts, ovaries, nectar, roots, exudate/gum, bark, leaves, whole fruits, pulp of beans, stems and seeds from fruits, legumes and grasses (Warren 2003). Aside from plants, invertebrates are regularly consumed, and one incident of an adult male baboon catching

and eating an infant bush buck was observed (pers. obs.). Overall, the group consume 119 identified food items, including fruits, flowers, seeds, leaves and invertebrates (Ross et al. 2009). Oil palm (*Elaus guineensis)* fruit is a staple food every month of the year, and poison wood tree seeds (*Erythrophleum suaveolens)* and aquatic invertebrates are both monthly staple foods for 7 months of the year (Warren 2003). Thus, while the environment at Kwano is marginal in terms of temperature and rainfall, there is a high abundance of food available.

The baboons have been habituated to the presence of human observers since 2000, and can now be approached and followed at a distance of 2-5 m. Apart from researchers and field assistants, they have little contact with humans.

Maternal Investment

The biggest decrease in the investment of olive baboon mothers has been recorded as between 10-12 months (Nash 1978), suggesting that this is when weaning is likely to take place. However, females in the Kwano group have unusually high inter-birth intervals at 25 months, and there is a high mortality rate among infants (Higham et al. 2009). Living on the edge of the species distribution and experiencing extreme environmental conditions (Higham 2006, Higham et al. 2009, Ross et al. 2011) may cause this detrimental effect on reproductive success. Closed canopy, humid forest environments with high levels of rainfall can lead to high levels of disease and parasites in adults (Ghandour et al. 1995) and some intestinal parasites are particularly prevalent among baboon infants (Müller-Graf et al. 1995), whose immune systems develop throughout the first year of life. It has been suggested that infants require specific weaning foods, i.e. those that are easy to obtain from the

ground and easy to digest (Altmann 1980) the abundance of which is not known at Kwano despite a generally high abundance of food (Warren 2003, Ross et al. 2009).

STUDY DESIGN

A pilot study was carried out from Jan – Apr 2010, to develop data collection protocols suitable for testing the hypotheses regarding activity budgets, infant handling, and vocal communication. During this time, data were collected from two troops of baboons in Gashaka-Gumti National Park for which long term data are available - Kwano troop, and Gam Gam troop, another habituated group of baboons with a home range close to Gashaka village. Gam Gam troop had few infants and no adult males at this time. Therefore, the feasibility of obtaining enough data to test the hypotheses in this group was low due to few potential focal animals. It was decided that Kwano troop would be the focus of the study, and data collection protocols were tested systematically only at Kwano. Here, morning and afternoon focal follows of 6 to 8 h durations were tested. The bulk of vocalisations were recorded first thing in the morning, and there were few instances of important behaviours such as infant handling and vocalisation sequences after 1200 hours, during the hottest temperatures of the day. It is unclear why this is the case, but this finding is consistent with a previous study into adult baboon vocalisations at Kwano (Ey 2008). Therefore, focal follows of infants of the Kwano group from 0600-1200 hours was chosen as the most suitable data collection method.

Following the completion of this pilot study, the main data collection phase ran from Oct 2010 to Apr 2011 in two blocks; Oct – Dec when it rained most days but was not peak rainy season, and Jan – Apr when it was dry. During this

time, SH collected all behavioural data, and volunteers Kerrin Gilbert (Oct - Dec) and Georgia Patey (Jan - Apr) collected audio recordings of all vocalisations. Data collection continued from Apr – Jul by Masters student Thomas Roberts (TR), who was trained to follow existing protocols in the field by SH. During TR's data collection, field assistant Maigari Ahmadu (MA) collected audio recordings of vocalisations. In addition to this main phase of data collection, Masters student James Thompson (JT) collected data on infant handling from Apr – Jul 2012. There are no audio data and no continuous behavioural observations available for this time, therefore data for one infant born in 2012 are only included in infant handling analyses (chapter 4).

Troop Composition

When data collection commenced in 2010, there were 31 individuals in the group, with 9 adult females, 1 sub-adult female, 6 adult males, 5 juvenile females, 5 juvenile males, 2 infant females and 3 infant males (age classifications, Tab. 02.01). A further 6 infants were born during the study period, and observations are available for 5 of these individuals, as one died within 24 hours of birth (full group composition, Tab. 02.02). Thus, data were collected for a total of 10 individuals. However, the number of infants for which

Tab. 02.01. Age classification of olive baboons (from Warren 2003, p. 291)

Classification	Age	Description
Black infant	0-7 months	Black coat, pink skin from birth. Skin changes to grey at 5 months. Ventral on mother from birth, dorsal from 4 months.
Infant	7 months to 2 years	Coat brown/grey/olive adult colour. Nurses occasionally
Juvenile female	2-4 years	Not in association with mother for majority of time. fully weaned
Subadult female	4-6 years	4 years + gradually gains height of adult female, onset of menarche. Tight red genital swelling
Adult female	6-8 + years	Usually have offspring, have longer nipples, which turn from pink to grey after nursing. Soft pale swellings. Nulliparous females considered adult if they show regular sexual cycle or engage in consortships
Juvenile male	2-6 years	Not in association with mother for majority of time. Fully weaned. Scrotum changes from pink to grey at 2-3 years. 5 years gain height of adult female, scrotum enlarges, canines extend beyond tooth row.
Subadult male	6-10 years	Larger than adult female, growth spurt continues, mantle and shoulder hair grows. May migrate in and out of group.
Adult male	10 years	Long sharp canines, mane of hair around neck and shoulders. About twice the size of adult female. Unbroken ischial callosities with a slightly raised centre line below tail

Tab. 02.02. Group composition, with approximate dates of birth where known. This table is approximate, and exact ages are used for all infant data analyses in subsequent chapters. Only infants served as focal animals, and all infants included in the study are listed as infants, though Dandy and Daji were weaned during data collection, and Emma and Eric developed from black infants to infants.

Code	Name	Age class	Sex	Mother
BRA	Bera	Adult	female	
DRK	Dr Kate	Adult	female	
FDI	Fadi	Adult	female	
KYE	Kaiye	Adult	female	
LDI	Ladi	Adult	female	
LMI	Lami	Adult	female	
MOM	Momi	Adult	female	
RAB	Rabi	Adult	female	
SDY	Sadiya	Adult	female	
YMK	Ymke	Adult	female	
MUR	Murna	Subadult	female	Ymke
AMY	Amy	Juvenile	female	Momi
ANN	Ann	Juvenile	female	Fadi
BNI	Beni	Juvenile	female	Dr Kate
BTH	Beth	Juvenile	female	Lami
TAL	Tala	Juvenile	female	Sadiya
DEB	Debbie	Infant	female	Ladi
DRS	Doris	Infant	female	Kaiye
DLI	Dali	Adult	male	
DRN	Darin	Adult	male	
ERN	Ernie	Adult	male	
KSA	Kasa	Adult	male	
SMA	Sama	Adult	male	
SND	Sanda	Adult	male	
BAK	Baki	Juvenile	male	Ladi
FAR	Faro	Juvenile	male	Kaiye
JMU	Jamilu	Juvenile	male	Bera
NAW	Nawa	Juvenile	male	Lami
DJI	Daji	Infant	male	Sadiya
DND	Dandy	Infant	male	Fadi
DMI	Dimi	Infant	male	Dr Kate
EGI	Eggi	Infant	male	Rabi
EMM	Emma	Infant	male	Ymke
ERC	Eric	Infant	male	Momi
ETO	Eto'o	Infant	male	Sadiya

data are available fluctuates between chapters due to differing data collection protocols between the 3 observers. JT used adult females as focal animals, therefore for one infant, only infant handling data observations were recorded, whereas full activity budgets are available for the remaining 9 infants.

All individuals can be identified by field assistants and have been allocated a three letter identification code. Field assistants follow adults in the group for 20 days per month, collecting data for a long term project to which this study will contribute. When an individual could not be identified during data collection due to poor visibility (e.g. they were too far away, or obscured by another individual) the following codes were used to provide data on age and sex:

A = ADULT (F = female, M = male)

S = SUB-ADULT

J = JUVENILE

Ib = BLACK INFANT (< 7 mo)

Io = INFANT (> 7 mo; colour brownish)

? = UNKNOWN AGE/SEX

Example: AM = adult male, JF = juvenile female, A? = adult unknown sex, Ib? = black infant unknown sex.

Data Collection

In order to explore infant socialisation in olive baboons, the handling of infants by adults other than their mother and the development of vocal communication have been identified as key. To investigate these phenomena, it is first necessary to quantify the 'baseline' behaviours of infants and adults in the group, to ascertain what these individuals are doing, and how long they are

doing it for. Once this is established, specific data on infant and adult behaviours associated with infant handling and the production of vocalisations can be used to describe the development of these behaviours, and infer its function. Therefore, during the 3 month pilot study carried out from Jan-Mar 2010, an ethogram (App. 02.01) and data collection sheet (App. 02.02) were developed. The ethogram defines all of the behaviours infants were seen to exhibit, such as feeding or playing, and all behaviours directed at infants, such as grabbing or grooming etc. As both baseline levels of behaviour and specific behaviours of short duration are of interest to the study of socialisation, continuous focal follows of the same animal were used, with additional all occurrence sampling of target activities (Altmann 1974). Focal sampling involves the selection of one individual as the primary focus of observation, and the recording all behaviours they exhibit. All occurrence sampling on the other hand, is the process of recording behaviours of interest whenever they occur. It is not a structured method of data collection like focal sampling, so both can be used at the same time. This combination was chosen to ensure that no rare behaviours or behaviours of short duration are missed.

Data collection protocols were used during focal follows of the same infant for 6 h periods, from 0600 – 1200 hours daily. A different infant was followed each day, and when the focal animal was lost (usually during river crossings in wet season) observations were either switched to another individual or terminated if less than half an observation day remained. The following section will describe how data were recorded in each section of the data collection sheet (cf. App. 02.02).

Morning Focal Follows

Producing comprehensive activity budgets was not a specific objective of this study, but rather assessing the changes in activity associated with ageing and the weaning process (for full list of objectives, see chapter 1, p.29). During the pilot study, the primary aim was to develop a data collection protocol that maximised the opportunity to record specific behaviours of interest such as vocalisations and infant handling. In order to record the maximum number of these events, the time at which most activity took place was chosen for focal follows. This was between the hours of 0600-1200. Therefore, activity budget data are not available for the entire day (with daylight hours at Kwano being approximately 0600-1700). If calculating the activity budgets of infants were the primary aim of this study, full day follows, or a mixture of early and late follows, would be essential for diurnal animals such as baboons (Altmann and Muruthi 1988, Dunbar 1992). However, using morning focal follows for infants of all ages still allows for an assessment of changes over time in behaviour such as maternal contact and nursing that are indicative of socialisation. This is the second study at Kwano to utilise 0600-1200 focal follows when aiming to study vocalisations, with the other focussing exclusively on environmental effects on adult vocalisations (Ey 2008).

Though observations from 0600-1200 were deemed the most appropriate method for this study, this of course restricts the certainty with which one can draw implications from activity budgets. While accurately representative of the time during which data were collected, the activity budgets presented cannot be generalised to represent an absolute measure of activity in the group. Thus, in line with the aims of the current study, activity budget data are treated as

indicative of infant activity during the time other data were collected, rather than as a representation of all infant activity. Therefore throughout this study, general levels of activity are presented as background information, and to assist in possible interpretations of other key data (see for example chapter 4, in which potentially high levels of nursing and infants being carried by mothers may offer insight into infant handling behaviour).

Furthermore, where comparisons to adults in the group are made, only the corresponding hours of adult activity budgets (0600-1200) are included. When comparisons to other populations are made, where possible, the hours for which activity budgets have been calculated in comparison studies are reported (this information was not available for all unpublished data). All activity budget data and comparisons with the activity of other populations are treated with caution, and interpreted as preliminary analyses.

Focal Animal Instantaneous Sampling

Instantaneous sampling was used to record the activity of the focal animal on the minute, every minute (Altmann 1974). This provides data to calculate an activity budget for each focal animal (chapter 3), showing how much time is spent involved in each activity within the observation period of 0600-1200 hours. On each minute marker, the location (forest or savannah) and height (0 to >10m) of the infant was recorded, to provide environmental context for the behavioural data. The following subsections describe the behaviours recorded during focal follows, with extracts from the ethogram (cf. App. 02.01).

State Behaviours

State behaviours (Tab. 02.03) are generally long in duration, and the total

duration of each behaviour was calculated in minutes, since state behaviours of the focal infant were only recorded on the minute marker (nb. all examples follow the protocol used in the field, in which capital letters are used for DESCRIPTIONS (location and animals) and lower case for behaviour events or states).

Tab. 02.03. State behaviours recorded during instantaneous sampling of focal animals, every minute on the minute.

BEHAVIOUR	**Additional Detail**
INFANT CLINGS	Actively holding an adult, either ventrally or dorsally
INFANT NIPPLE CONTACT	Used as a proxy for nursing, which often cannot be determined
INFANT RIDES	Sitting dorsally on the back of an adult
FEEDING	Eating food independently of mother
GROOM	Including who is grooming whom
LOCOMOTE	Walking or running
PLAY ALONE	Playing more than 1m from another individual
PLAY SOCIAL	Playing within 1m of another individual
PLAY LOCOMOTE	Running, jumping etc.
PLAY OBJECT	Interaction with sticks, leaves etc.
PLAY ROUGH	Play fighting including biting and wrestling
REST ALONE	No other individual within 1m
REST SOCIAL	Within 1m of another individual

Company

The identity of other individuals close to the focal animal was also recorded using instantaneous sampling. Company is defined as all individuals < 1m (approximately touching distance) from the focal animal. The identities of the individuals close to the infant were recorded when known. When identities were not known, in addition to the age and sex codes described previously, the 'company' category can also contain the following data:

A = ALONE

M = MOTHER

P = PEER, another infant, PM or PF, P?

c = CONTACT, addition of c if there is body contact

n = NIPPLE CONTACT WITH MOTHER

Example: Mc = mother body contact, JM = juvenile male, no contact.

All Occurrence and Ad Libitum Sampling

All occurrence sampling involves recording all instances of a behaviour, whenever it occurs (Altmann 1974). Some of these are events (e.g. grab; Tab. 02.04), and some are states that can last for several minutes (e.g. groom; cf. Tab. 02.03). For the particular behaviours that this study is focusing on, infant handling and vocalisations, all occurrence sampling of focal animals is appropriate as it ensures that all instances of these often short events are recorded. When of a short duration, such behaviour events were recorded as the number of times that they occurred within each minute, in the form of a tally, rather than by duration as per state behaviours. Many behaviours described here (cf. Tab. 02.03, Tab. 02.04) have been identified as important

in socialisation (groom, hold, muzzle contact, lip smack and approach; Coehlo and Bramblett 1984) mother-infant interactions (infant clings, infant rides, infant nipple contact; Rhine et al. 1985, Altmann 1988, Nicolson 1982, Muruthi 1997) and infant handling interactions (grab, hold, embrace, groom; Henzi and Barrett 2002). Vocalisations included in the ethogram were based on previous descriptions of adult (grunt, wahoo, scream; Rendall et al. 1998; Owren et al. 1997, Fischer et al. 2001) and infant (geck, scream, moo; Byrne 1981, Wallez and Vauclair 2012) baboon vocal repertoires, although far greater detail on the infant vocal repertoire is presented in the current study (chapters 5 and 6).

Additionally, ad libitum sampling of infant handling and vocalisations was carried out for non-focal infants, if such events were noticed nearby (<5m) and recording them did not affect focal data collection. Thus, a combination of instantaneous and all occurrence sampling was used to record focal animal behaviour, while ad libitum sampling was used for other infants within 5 m of the focal animal for behaviours of particular interest. The remainder of event behaviour categories (cf. Tab. 02.04) are central to dominance interactions, describing displacements and aggressive interactions that are recorded routinely as part of long-term data collection at Kwano Field Station, and used to construct the dominance hierarchy for this group. Therefore, while not a priority to the aims the current study into infant socialisation and sometimes hard to notice in non focal animals (e.g. bare teeth, displace), these data were collected ad libitum for all individuals of all age classes within 5 m of the focal animal whenever they were noticed and it was practical to do so without disrupting focal data collection, in order to make a valuable contribution to the dominance hierarchy used in subsequent analyses.

Tab. 02.04. Behaviours recorded using all occurrence sampling for focal animals, and ad libitum sampling for non-focal animals within 5 m of the focal animal.

BEHAVIOUR	Additional Detail
APPROACH	A moves directly towards B, and stops <1m or begins social interaction
BARE TEETH	Lips vertically retracted, with mouth either open or closed
EMBRACE	Contact with another individual without grasping
GROOM	Including who is grooming whom
PRESENT	presentation of anogenital area to another individual
FOLLOW	Locomotory action of shadowing a recipient animal
GRAB	Grasping any portion of another animal's body without maintaining grip
HOLD	Grasping any portion of another animal's body with a maintained grip
MOVE AWAY	Moving >1m away during or after an infant handling attempt
LIP SMACK	Rapid repetitive opening and closing of lips
DISPLACE	A yields position to B
MUZZLE CONTACT	Placing of the muzzle to or the muzzle of a recipient
CHASE	Running after another individual
SLAP	Slapping another individual aggressively as opposed to rough play
BITE	Biting another individual aggressively, as opposed to rough play
GRUNT*	Low pitched adult vocalisation
WAHOO*	Two syllable vocalisation produced by adults and older infants
SCREAM*	High pitched, highly variable vocalisation produced by all age classes

*Full definitions of all vocalisations, chapters 5 and 6

All occurrence and ad libitum data were recorded as a narrative, with the behaviour and identities of those involved, enabling one to reconstruct everything that happened in its correct sequence (Fig. 02.08). Approximate duration of state behaviours was recorded by noting when it continued into the following minute time slot, as per the focal behaviours described previously. Unrelated events, those involving different individuals, were recorded with a full stop separating them, and commas were used between separate behaviours of the same sequence.

	FOCAL ANIMAL INSTANTANEOUS				ALL OCCURRENCE AND AD LIB (ALL INDIVIDUALS <5M)	
	AREA	STATE	HEIGHT	COMPANY	EVENTS	BYSTANDER
1	F	cl	0	DRKc		
2	F	lo	0	BNI	LMI pre DRK, vg |||, LMI gr DRK	
3	F	cl	0	DRKc, LMI	LMI gb DMI	DLI

Fig. 02.08. Example of a completed data collection sheet, showing how a combination of focal, all occurrence and ad libitum sampling was used to record the behaviour of infants and other group members.

The above example (Fig. 02.08) represents the following narrative:

Min 1: In the forest, on the ground, focal infant Dimi is clinging, in body contact with his mother, Dr Kate.

Min 2: In the forest, on the ground, Dimi is locomoting with juvenile female Beni nearby. Within the minute, Lami, an adult female, presents to Dr Kate, then grunts three times. Lami then grooms Dr Kate.

Min 3: In the forest, on the ground, Dimi is clinging, in body contact with Dr Kate. Grooming continues into this minute slot, and Lami grabs the Dimi. Dali, an adult male, is a bystander when this attempt to handle the infant occurs.

Sound Recordings

Audio recordings were made of as many vocalisations produced by the focal infants as possible, as well as ad libitum recordings of adult vocalisations directed at the infant (e.g. grunts preceding infant handling). Recordings were made using a Marantz P660 Solid State Recorder with a Sennheiser ME66 directional microphone. These vocalisations were recorded by volunteers, so that it was possible to collect behavioural and audio data simultaneously. The reference number of each audio file was noted in the narrative of behaviour, so that context could be analysed alongside acoustic data (chapter 5). This way, state, event and audio data were recorded for focal infants and other group members nearby.

Data Analysis

Due to differing data collection methods for each variable of interest, in addition to descriptive statistics, a range of parametric and non-parametric statistical analyses have been used. For example, ANOVAs were deemed appropriate to compare the mean percentage of different infant handling behaviours, and can reveal differences in the relative rank of mothers and handlers. For categorical variables, such as comparing the relationship between 'did grooming occur: yes/no', and 'was infant handling aggressive: yes/no', X^2 or fisher's exact tests have been used, depending on sample size. For all of these tests, a p value of 0.05 was considered a significant result. Where applicable, all tests were 2-tailed. In addition to these analyses,

generalized linear mixed models (GLMMs) have been used to control for multiple sampling for the same individuals for both activity budget and infant handling data (Waller et al. 2013).

Cross-validated discriminant function analyses were used to assess whether the selected acoustic variables could account for a significant amount of the variation in the data set, and to show how many calls could be correctly classified as, for example, male or female. Binomial tests were then used to assess whether the number of calls correctly classified was significantly different from chance. Further permuted discriminant function analyses were then carried out to control for multiple sampling of the same individuals (Mundry and Sommer 2007; Waller et al. 2013). Here, the number of correctly classified calls is compared to a random (actually permuted) distribution of test statistics, therefore binomial tests are not provided.

Long Term Data Collection

In addition to the data collected as part of this study, data that are continuously collected by field assistant Halidu Iliyasu (HI) for Roehampton University, were used to assess the effects of a range of variables upon infant behaviour.

HI follows a different focal animal each day, and uses scan sampling every 15 minutes to determine which individuals are nearby, recording their nearest neighbour, those within 2 m, those within 2-5 m, and those more than 5 m away. At the same time, ad libitum sampling of aggression and displacements were recorded. These data were used to establish a dominance hierarchy for the group.

Limitations

Only 10 infants were present in the study group between 2010 – 2012, and at times, fewer were classified as infants as two infants were weaned during the study period. While this is a small sample, data were available for all individuals who were classified as infants when the study began and four who were born during that time, therefore the 10 infants for whom data are available represent all live births from 2009 – 2012. The small sample size may be an unavoidable result of studying a group in a marginal environment with high inter-birth intervals and a high infant mortality rate. In fact, two of the infants for whom a substantial amount of data are available died after data collection had ended, and one infant died less than 24 hours after birth. Therefore, while the small sample size is a limiting factor in terms of generalising from the analyses presented here, it may be the only way to study infant behaviour in a marginal environment. In addition to the small sample size, there is also a strong gender bias. All four infants born during the main study period were male, so it was not possible to test for gender differences in the behaviour of infants aged 3 months or younger.

Summary of Data Collected

The following section summarises the data collected to test each set of hypotheses, which will then be presented in detail in subsequent chapters together with data analyses. SH made a total of 341 hours of focal observations across 9 individuals observed since October 2010; approximately 19000 instantaneous observations of state behaviour in total (Tab. 02.05). Together with 70 hours of focal follows by TR in 2010, this makes an overall total of 411 hours of observations; approximately 23000 instantaneous

observations from which to calculate activity budgets (chapter 3). While the sample size was small, the behaviours that are key to this study were common during the focal observation hours. Therefore, even with only 10 focal animals, 2007 instances of infant handling (Tab. 02.06), 188 vocalisation bouts (Tab. 02.07), and more than 2500 audio files of vocalisations were recorded.

Tab. 02.05. Observation hours per individual, for data collected between Oct 2010-Apr 2011 by SH. ELE was the only individual not observed by SH, and for whom only ad libitum infant handling data are available.

Focal Animal ID	Date of Birth	Sex	Observation Hours	On-the-dot observations (approx.)
DND	08-Feb-09	M	31	1846
DJI	03-Aug-09	M	20	1174
DRS	21-Aug-09	F	49	2744
DEB	31-Aug-09	F	50	2800
DMI	12-Dec-09	M	60	3360
EMM	est. 15-Sep-10	M	75	4200
ERC	est. 15-Oct-10	M	74	4144
ETO	01-Mar-11	M	26	1456
EGI	06-Mar-11	M	26	1456
ELE	est. 01-Jan-12	F	Ad libitum only	Ad libitum only

Tab. 02.06. Instances of infant handling per individual (for definition of infant handling, see chapter 4).

Focal Animal ID	Date of Birth	Sex	Infant Handling
DRS	21-Aug-09	F	32
DEB	31-Aug-09	F	36
DMI	12-Dec-09	M	8
EMM	est. 15-Sep-10	M	317
ERC	est. 15-Oct-10	M	257
ETO	01-Mar-11	M	517
EGI	06-Mar-11	M	528
ELE	est. 01-Jan-12	M	312
Total			2007

Tab. 02.07. Number of vocalisation bouts recorded per individual (for definitions of vocalisations and vocalisation bout, see chapters 5 and 6).

Focal Animal ID	Date of Birth	Sex	Vocalisation Bouts
DRS	21-Aug-09	F	31
DEB	31-Aug-09	F	10
DMI	12-Dec-09	M	27
EMM	est. 15-Sep-10	M	49
ERC	est. 15-Oct-10	M	66
ETO	01-Mar-11	M	3
EGI	06-Mar-11	M	2
Total			188

CHAPTER 03:

ACTIVITY BUDGETS: A DAY IN THE LIFE OF A BABOON

View of Gashaka Gumti National Park at sunset, from Kwano field station.

Photo: Suzanne Harvey 2011.

INTRODUCTION

While the social activities of baboons are often seen as the most interesting behaviours, and of course vital to the study of infant socialisation, these comprise a relatively small percentage of daily activity (e.g. Altmann 1980). In order to investigate infant socialisation, in addition to the special cases of infant handling and vocal communication, the basic differences between infant and adult activity budgets are also relevant. Most studies of baboon activity budgets have focused on changes in adult behaviour under social or environmental pressure, such as sexual consortships in olive baboons (Bercovitch 1983) and yellow baboons (Rasmussen 1985; Alberts et al. 1996), predation risk in chacma baboons (Colishaw 1997) and food provisioning in yellow baboons (Bronikowski and Altmann 1996).

The effects of motherhood on activity budgets have also been assessed, leading to a theory of maternal time budgets that predicts an increase in the time mothers spend feeding as their infants age, with a corresponding decrease in social activities (Fig. 03.01; Altmann 1980). This theory has also been assessed in gelada baboons (Dunbar and Dunbar 1988), where it was found that while infants required more maternal investment, mothers preserved their social time above all other activities, and time spent resting was reduced instead. The link between an infant's need to nurse and its ability to feed, and the consequent effects on other behaviour, is strongly linked to socialisation. This culminates in the onset of weaning and subsequent transition from infant to juvenile.

Weaning

The preferred activities of an infant may not always be compatible with those of its mother, as both aim to maximize their own fitness. The concept of inclusive fitness (Hamilton 1964) in which parental support of offspring is considered important to fitness as well as the overall number of births, is particularly relevant to the weaning of infants (Galef 1981; Promislow and Harvey 1990).

Fig. 03.01. Infant male Emma in nipple contact with his mother Ymke, at 5 months of age. (Photograph: Suzanne Harvey, 2011.)

For example, since lactation presents one of the highest costs of reproduction (Clutton-Brock 1991), a mother will benefit from weaning infants as early as possible. There are strong correlates between weaning weight and juvenile mortality (Promislow and Harvey 1990). This suggests that infants must reach a critical weaning weight prior to being weaned (Lee 1996; Zhao et al. 2008). A mother's most successful reproductive strategy will be to find a balance between feeding infants long enough for them to survive, and weaning each infant early enough to conceive another (Trivers 1974; Clutton-Brock 1991). Females should maximize the number of infants surviving to adulthood and reproducing themselves, thus overinvesting in one infant and nursing it for longer than necessary is not beneficial. Each of her infants, on the other hand, will simply want to maximize its mother's level of investment, nursing and supplementing its diet with milk for as long as possible. This 'evolutionary conflict' (Altmann 1980) manifests itself in behavioural conflicts that are discussed in detail in chapters 5 and 6. Here, the resultant changes in activity with age are described.

While the effect of environment on female reproductive success has been documented, the development of the infants themselves has not been previously assessed. Therefore, the aim of this chapter is not only to describe the activity budgets of infants from birth to weaning, but also to compare the activity budgets of infants in the Kwano group with those of baboons of the same age at other study sites. It is predicted that, given the long inter-birth intervals of females (chapter 2), Kwano infants will be dependent upon their mothers for longer than those of other groups. Specifically, Kwano infants are expected to be carried by their mothers for longer than other infants, and be

weaned later, due to the increased maternal investment required in a marginal habitat. Where possible, a comparison of infant activity budgets in wet and dry seasons has been made, since environment has been shown to affect adult activity budgets. This is necessary to avoid erroneously attributing all behavioural changes to socialisation, when basic environmental factors such as rainfall are known to affect behaviour in the Kwano group (Warren 2003).

For comparison to infant activity budgets, data collected by JT on the activities of adult and sub-adult females in the group is also presented. The resulting description of how infant behaviour changes over time, including variation in the time an infant spends in contact with its mother, and the onset of weaning when the ratio between nursing and independent feeding changes dramatically, provides a baseline of behaviour by which to understand communication patterns (chapters 5 and 6). These data will also provide a baseline activity level from which to assess the effects of infant handling.

Defining Weaning

Many studies, including several of those used as comparison studies in this chapter (Altmann 1998, Muruthi 1997, Rhine et al. 1985) use 12 months of age as a cut off point when studying the weaning process, defined as the gradual cessation of sucking and acquisition of foraging skills (Altmann 1998, Rhine et al. 1985, Nicolson 1982, Humphrey et al. 2007). However, nursing often continues beyond this point (Lee 1996, Martin 1984) and for some populations, data on the rate of nursing are available for older infants (Altmann 1998, Nicolson 1982). Moreover, the age of weaning varies within populations (Lee 1996) and has been more closely linked to infant growth than a range of other

variables including maternal size and neonate weight (Lee 1996, Lee et al. 1991).

For this reason, a cut-off point of a year seems somewhat arbitrary, and certainly not sufficient for a study investigating infant socialisation, since changes in nursing behaviour continue after infants reach one year of age. Therefore, rather than selecting a predetermined age at which an individual was no longer a focal animal, each individual was considered an infant (and thus a focal animal) until fully weaned. This was classed as not nursing at all for two full, consecutive observation days. When this occurred, SH additionally checked whether any field assistants had observed the individual nursing outside of focal follows, and if not, that individual was classed as weaned. Using these criteria, two infants were classed as weaned during this study (Dandy and Daji, both male aged 22 and 23 months).

While the time of absolute dietary independence was considered important, another key phase in the weaning process is the point at which maternal investment declines most rapidly (Martin 1984, Roberts 2011) and this has been observed as between six and eight months in baboons (Nicolson 1982). While observations continue after this point, this remains key to the mother-infant conflict perspective, and indeed formed the context of many physical conflicts between mothers and infants that resulted in vocalisations that form a tantrum display (Altmann 1980; 'refused nipple' context, chapter 6). Therefore, while there is some debate over the definition of weaning, in the current study a complete cessation of nursing is considered an appropriate definition, while acknowledging that a significant reduction in maternal investment will take place at a much younger age.

MATERIALS AND METHODS

Data Collection

Focal follows of infants were carried out by SH and TR from 0600-1200 hours daily, and a different infant was followed each day. The order in which the focal animals were followed was random, but the number of focal follows was intended to be as equal as possible across all individuals. Therefore if there were 5 infants in the group at the time, each was followed once every week, but on a random day of the week. State behaviours were recorded every minute, on the minute. Contact with mother recorded as either 'infant clings' or 'infant rides', (Fig. 03.02) and 'nipple contact' (cf. Fig. 03.01) was used as a proxy for nursing (full definition of behaviour categories, Fig. 02.02., Fig. 02.03; ethogram App. 02.01).

Of the four individuals for which data are available from birth, two were born in Sept and Oct 2010 (wet season), and two were born in Mar 2011 (dry season). More data are available for infants born in dry season, due to greater visibility (high grasses can obscure infants in wet season) and greater success locating the group each day.

Fig. 03.02. Infants being carried by their mothers, either clinging (top) or riding dorsally (bottom). (Photographs: Suzanne Harvey, 2011.)

Adult Focal Follows

Focal follows of adult and sub-adult females were carried out by JT from Apr - Jun 2012, between the hours of 0600 and 1700. During this time, a number of studies with Kwano troop as their focus were taking place simultaneously, therefore focal follows of varying length, up to a maximum of 60 min were used (mean 34 min). Upon locating a subgroup of baboons, a suitable focal animal was identified with reference to the number of observation hours already taken. This allowed for a high degree of balance throughout the research period. At the end of a focal follow another suitable focal animal was located and the process repeated.

Only adults or sub-adults who were not nursing an infant were included in the sample, therefore the altered activity budgets of mothers observed in other studies did not constitute a confounding variable. Adult behaviour was documented using the same ethogram and data collection sheet as for infant focal follows, therefore, with the exception of behaviour such as nursing that is only seen in infants, comparable data on state behaviours were collected for both adults and infants.

Data Collection Protocols at Comparison Sites

Few studies have investigated infant carrying and weaning in baboons, and some of those remain unpublished (e.g. Nicolson 1982, Muruthi 1997) or contain insufficient information on data collection protocols for a direct comparison with the current study (Tab. 03.01). In light of these differing data collection protocols, and the controversy surrounding the ‘progressions’ method, in which each infant’s state behaviour is recorded when it passes

between the observer and an arbitrary stationary point, such as tree (Rhine et al 1985, Rhine and Westlund 1981) no inferential statistics have been carried out on these comparison data. Instead, an illustration of the patterns of change is shown (Fig. 03.10, 03.11). Figures are partially reproduced from Altmann (1997) with permission.

Tab. 03.01. Data collection protocols in four comparison studies

Study	Study Site	Subspecies	Sample Size	Collection Protocol
Muruthi 1997*	Amboseli	Olive	Unpublished	Focal sampling
Nicolson 1982*	Gilgil	Olive	Unpublished	Point sampling
Rhine et al. 1985	Mikumi	Yellow	55	Progressions (Rhine and Westlund 1981)
Altmann 1998	Amboseli	Yellow	Range: 2-11	Focal sampling
Altmann 1988	Amboseli	Yellow	Range: 2-11	Focal sampling

* Data included in both contact time and nipple contact comparisons

Analyses

Analyses are based on 283 hours of observation of 9 infants, aged 0-22 months. Data are not available for all 9 individuals for every month of life, and are necessarily unevenly distributed due to differing ages of individuals at the start of the study, and additional births (Tab. 03.02). Data were input into R version 3.0.2, GUI 1.62 Snow Leopard build for further analyses, and statistics were carried out on counts of each behaviour per individual, per age group (3 monthly groups). For these analyses, N = 27, representing one data point for each individual, in each age group to which they contributed (cf. Tab. 03.02).

Subsequently, Generalised Linear Mixed Models were carried out with individual entered as a random factor, to avoid the pseudoreplication caused by multiple observations of each individual. These were also offset for observation time.

Monthly activity budgets were then compared to data from other study sites, including both olive baboons at Amboseli (Muruthi 1997) and Gilgil (Nicolson 1982) and yellow baboons (Papio cynocephalus) at Amboseli (Muruthi 1997; Altmann 1998) and Mikumi (Rhine et al. 1980). Due to differing data collection protocols between these studies (Tab.03.01) and the morning focal follows used in the current study (for detail, see chapter 2) comparisons only serve to contextualise the results of the current study, and it is not possible to draw strong conclusions about differences in activity budgets at different field sites.

In order to effectively visualise such comparisons, rates of activities were calculated, as opposed to the counts of behaviours used to carry out GLMMs and in visualisations of individual behaviour categories (Figs. 03.03 – 03.06). First, data for all individuals were combined. Then, for each month of life, the number of observations of each behaviour state were divided according to the hour of the day (0600-1200). Within each hour, the percentage of observations of each state behaviour was then calculated. For example, for hour 8, month of life 1, 112 of 396 instantaneous observations of state behaviour were classed as ‘infant clings’. Thus, infant clings accounted for 28% of observations. The mean percentage of each behaviour was calculated across all hours of observation, giving an average for all individuals throughout the observation period (0600-1200) per month of life. This method produces rates of behaviours that can be used to visually compare data from different

populations, and data collected in wet and dry seasons (Figs. 03.07 – 03.10) but would not be suitable for inferential statistics as grouping all individuals in this way creates issues of pseudo-replication. Therefore, such rates are only used to present data that are not suitable for inferential statistics anyway, due to differing data collection protocols (data from different study sites) or small sample sizes (wet and dry season data). Where inferential statistics have been carried out, all visualisations represent the counts of behaviours used to calculate GLMMs rather than rates of behaviour calculated as described here.

Finally, a comparison was made between infant and adult/subadult activity budgets at Kwano. For these analyses, while adult and subadult focal follows were carried out between 0600-1700, only observations made between 0600-1200 were included, so that all behaviours of infants, adults and subadults were recorded during the same hours. Here, the mean percentage of each behaviour was calculated across all hours of observation, giving an average for all individuals throughout the relevant observation period (0600-1200).

RESULTS

Activity budgets broadly show the expected pattern of an increase in independent locomotion, independent feeding and social behaviour with age (Tab. 03.02).

Tab. 03.02. Time spent engaged in the most common activities (counts) for all focal animals (N = 9) by month of life. Composite categories are: rest (social and alone); play (social, alone, rough, and substrate); groom (active and passive); carried by mother (cling and ride). These data were used to calculate all GLMMs.

Individual	Age	Rest	Play	Groom	Carried by mother	Nipple Contact	Independent feeding	Locomote	Total
Dimi	1-3	16	8	2	76	6	11	4	123
Eggi	1-3	137	4	3	238	469	6	99	956
Emma	1-3	220	107	5	259	58	1	56	706
Eric	1-3	177	35	4	482	79	14	57	848
Eto'o	1-3	107	14	3	131	537	22	150	964
Dimi	4-6	127	34	25	495	53	107	62	903
Emma	4-6	214	67	15	509	274	38	186	1303
Eric	4-6	87	21	3	681	169	49	101	1111
Debbie	7-9	150	105	14	527	97	100	68	1061
Dimi	7-9	131	137	28	132	69	149	128	774
Doris	7-9	66	99	15	257	58	109	116	720
Emma	7-9	32	10	5	335	132	56	77	647
Eric	7-9	4	17	2	122	16	2	16	179
Debbie	10-12	70	89	23	263	82	154	105	786
Dimi	10-12	49	2	5	0	5	77	17	155
Doris	10-12	143	165	38	101	80	316	249	1092
Dandy	13-15	7	9	0	0	0	33	24	73
Dimi	13-15	66	11	30	0	42	235	169	553
Dandy	16-18	271	127	27	24	56	393	290	1188
Debbie	16-18	217	49	67	0	17	586	463	1399
Dimi	16-18	213	41	21	0	53	421	451	1200
Doris	16-18	122	17	41	0	40	350	263	833
Daji	19-21	119	105	8	0	17	200	107	556
Dandy	19-21	14	28	0	0	0	32	32	106
Debbie	19-21	31	15	8	1	1	207	177	440
Doris	19-21	117	24	39	0	122	373	360	1035
Daji	22	68	55	7	1	12	143	120	406

Contact and Independence

Data were grouped into three-monthly categories, to even out short-term fluctuations in behaviour. A Generalized linear Mixed Model (GLMM), with individual identity entered as a random factor, was carried out to investigate whether time spent being carried by mother (a count for each individual, in each age category; Tab. 03.02) was affected by age (3-monthly categories). This confirmed that age class significantly affected the amount of time spent

being carried (X2 = 1200.2, N = 27, df = 3, p = <0.001). Though there was a peak at 4-6 months (Fig. 03.03), overall, infants spent less time being carried by their mothers as their age increased (est = 0.66, SE = 0.02, z = -30.73, p = <0.001).

The early peak corresponds with a decrease in nipple contact at 4-6 months, possibly reflecting a lack of locomotor independence at this age. A further GLMM confirmed that age class significantly affected the amount of time spent in nipple contact (X2 = 7.52, N = 27, df = 3, p = <0.006). Infants spent less time in nipple contact as their age increased (est = -0.06, SE = 0.02, z = -2.79, p = <0.005), though nursing continued at low frequencies at 19-21 months. There were 152 observations of 4 individuals' nursing behaviour between the ages of 19-22 months, though these data were unevenly distributed and one individual accounted for 122 observations. One infant this age was not seen to nurse while 3 were (cf. Tab. 03.02). Age class also significantly affected the amount of time spent feeding independently (X2 = 508.91, N = 27, df = 3, p = <0.001). Infants spent more time feeding independently as their age increased (Fig. 03.04; est = 0.26, SE = 0.01, z = 21.92, p = <0.001). The decrease in independent feeding at 19-21 months may be due to a lack of data in this age group, with the one individual accounting for a large proportion of observations in this age class (cf. Tab. 03.02).

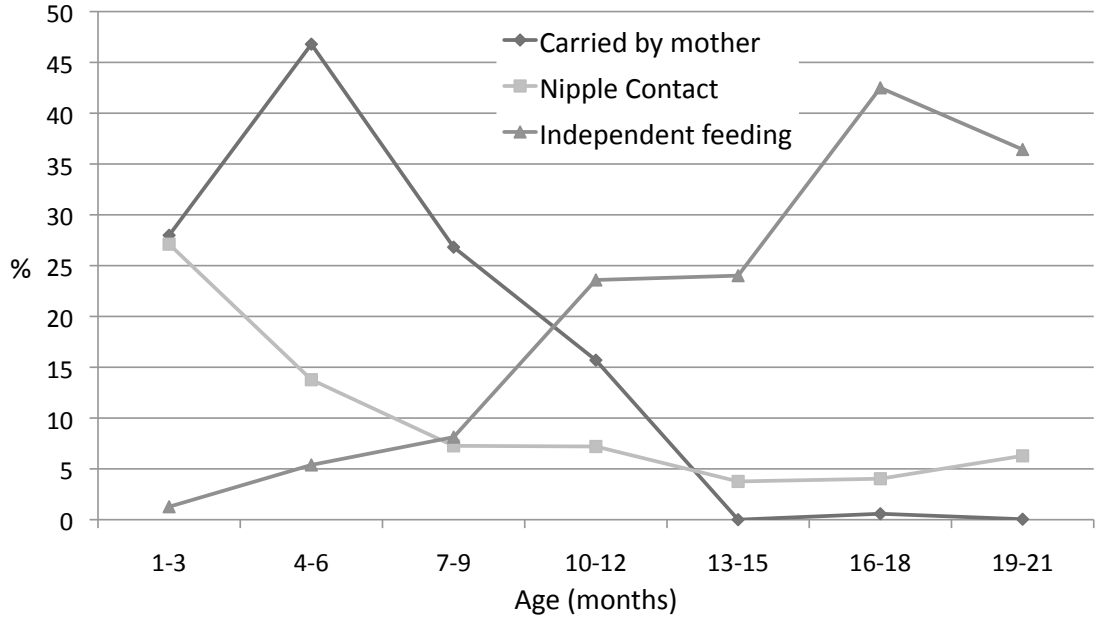

Fig. 03.03. Time spent being carried by mother or nursing, versus independent feeding. Data represent the average percentage of observations for all individuals grouped.

Age class also significantly affected the amount of time spent locomoting independently ($X^2 = 590.6$, N = 27, df = 3, $p = <0.001$), with infants generally spending more time locomoting independently as their age increased (est = 0.29, SE = 0.01, z = 23.33) although this was not a linear relationship (Fig. 03.04). In fact, months 10-12 and months 13 onwards contradict this trend. Though age class significantly affected time spent resting ($X^2 = 4.65$, N = 27, df = 3, $p = 0.031$), the trend for a decrease in time spent resting as age increased was not strong (est = -0.03, SE = 0.02, z = 0.03). Across the first three age classes, time spent resting more than halves from an average of 16% to an average of 7%, but there are marked fluctuations thereafter (cf. Fig. 03.04).

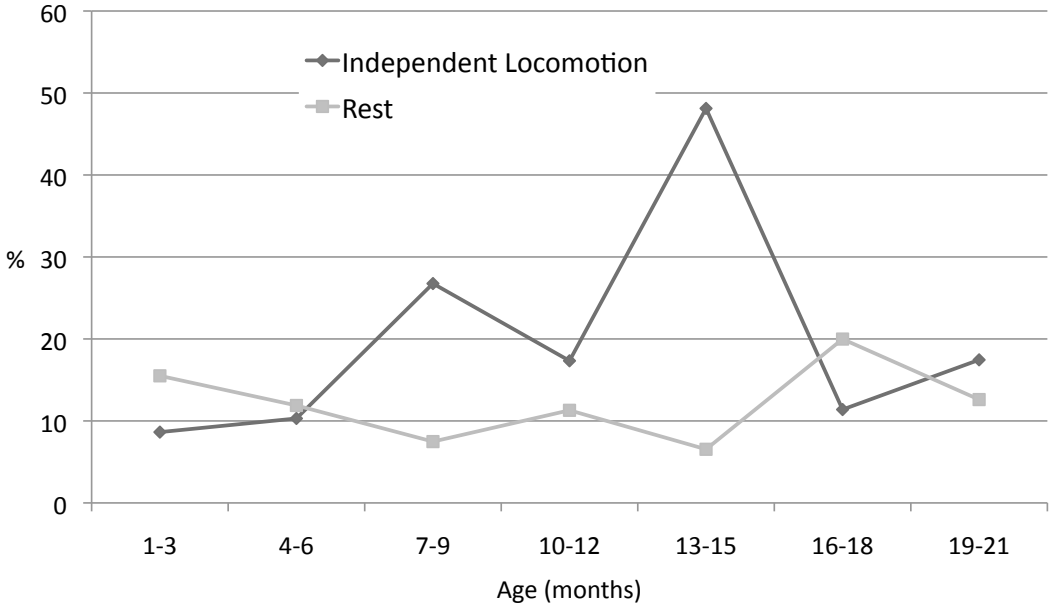

Fig. 03.04. Time spent being locomoting independently versus resting by mother or nursing, versus independent feeding. Data represent the average percentage of observations for all individuals grouped.

Rest

When rest was broken down into its constituent categories of 'rest social' and 'rest alone', there was a marked difference between the two types of rest in almost all age categories (Fig. 03.04). Both were significantly affected by age ('rest alone': $X^2 = 109.23$, $N = 27$, $df = 3$, $p = <0.001$; 'rest social': $X^2 = 194.42$, $N = 27$, $df = 3$, $p = <0.001$), and the model suggests that infants spent less time resting socially as their age increased (est = -0.28, SE = 0.021, z = -13.59 p = <0.001), whereas they spent more time resting alone as their age increased (est = 0.24, SE = 0.024, z = 10.22, p = <0.001). However, this is clearly not a straightforward linear relationship (cf. Fig. 03.05). Overall, infants less than three months of age spent on average less than 1% of their activity budget resting alone.

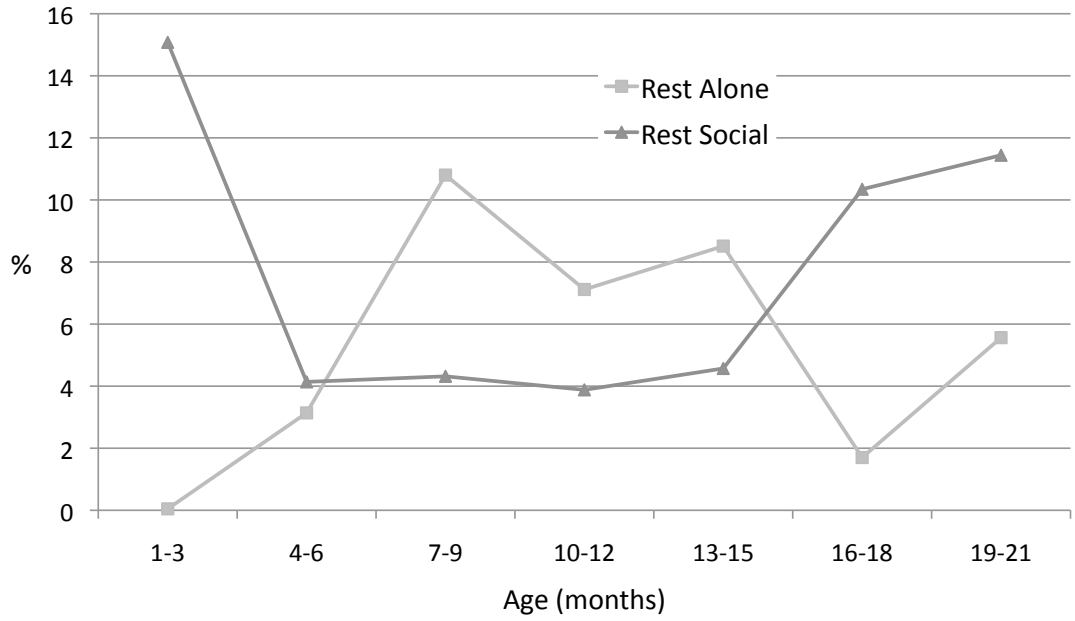

Fig. 03.05. Time spent resting alone and resting socially, defined as within one metre of another individual. Data represent the average percentage of observations for all individuals grouped.

Grooming

Although grooming interactions did not exceed 4% of infants' activity budgets at any month of age, and remained at less than 2% until 10 months of age, time spent grooming (a composite of 'grooming' and 'being groomed') was nevertheless significantly affected by age ($X^2 = 10.00$, $N = 27$, $df = 3$, $p = <0.002$). Infants spent more time grooming as their age increased (est = 0.11, SE = 0.03, $z = 3.27$ $p = <0.001$), though again this relationship is not linear (Fig. 03.06).

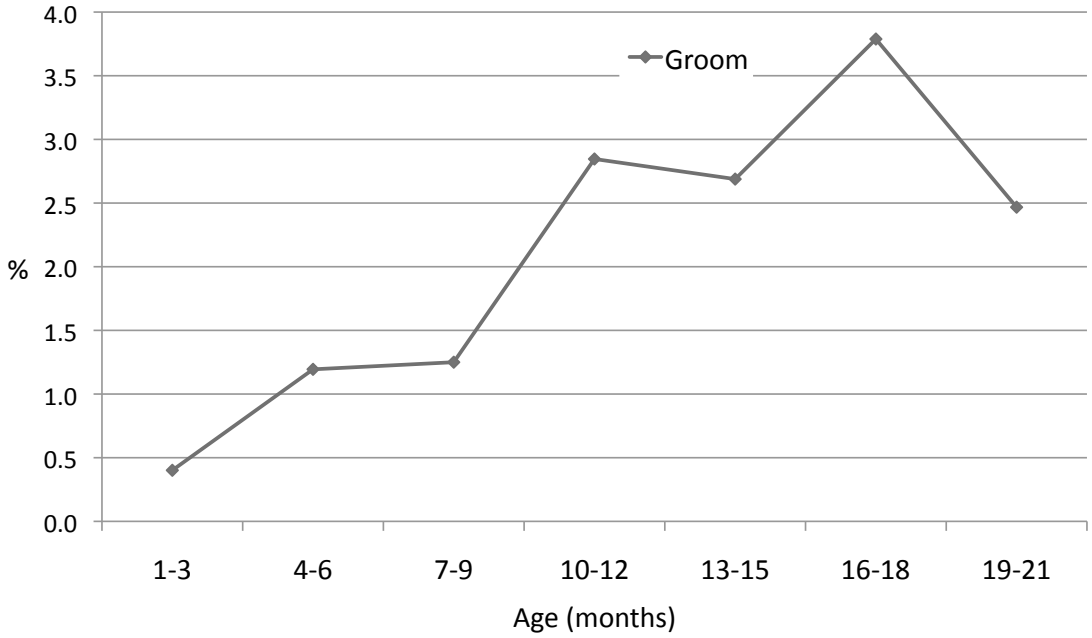

Fig. 03.06. Time spent grooming or being groomed. Data represent the average percentage of observations for all individuals grouped.

Activity Budgets in Wet and Dry Seasons

Though data were not available for a full comparison of behaviour in wet and dry seasons, infants born in the first and second years of observations allowed for preliminary analyses of seasonal differences. There were sufficient data available to make a direct comparison between month of life 1 and 2 for infants

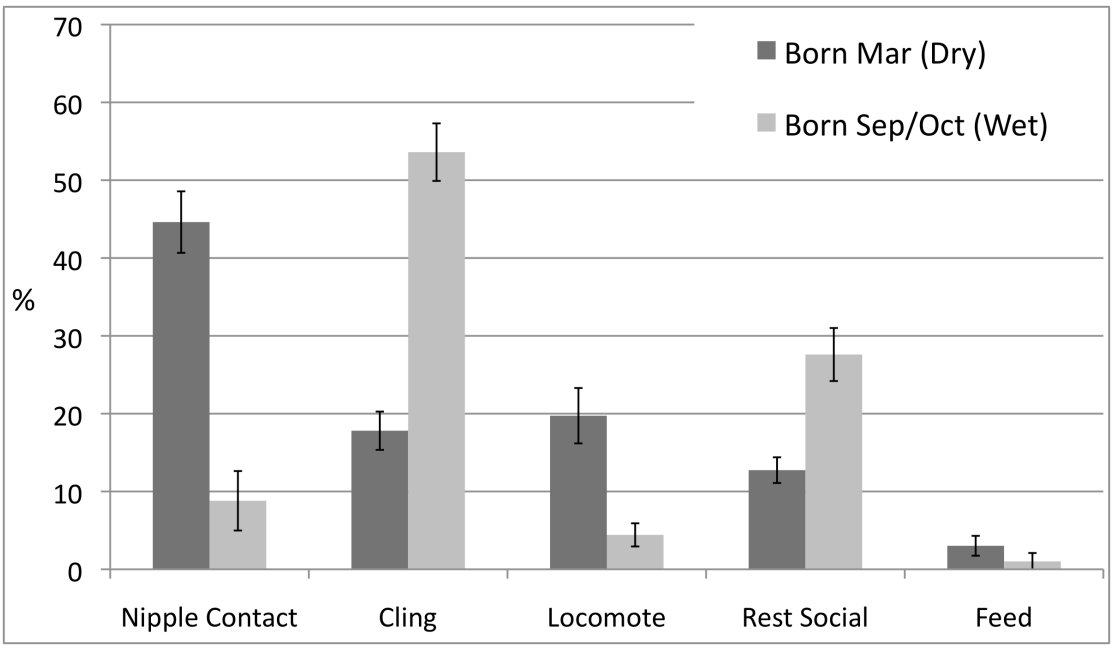

Fig. 03.07. Activity budgets for 4 individuals aged 0 - 2 months, born in either the wet (N=2) or dry season (N=2). Bars indicate mean ± standard deviation.

born in wet and dry season (Fig. 03.07). Only categories that comprise 5% or more of activity budgets were included, with the exception of independent feeding, as this was uncommon in the first months of life but crucial to testing the hypotheses. Here, the category 'cling' is not combined with 'ride' as per other analyses, as infants do not ride on their mother's back in the first two months of life; therefore, clinging represents all contact with the mother that is not nipple contact.

Though sample sizes are too small to carry out inferential statistics, descriptive statistics suggest that in the first three months of life, infants spent more time in nipple contact in dry season than in wet season, and less time clinging to their mothers in dry season than in wet season. At this age, infants in dry season also spent more time locomoting independently than those in wet season. In this age group, 20 hours of observations were available in wet

season (N = 2 individuals), and 29 in dry season (N = 2 individuals). The data are not evenly distributed across wet and dry seasons due to increased difficulty in observing infants in long grass during wet season.

There were also sufficient data to compare behaviour in months 5-7 in wet and dry seasons (Fig. 03.08). Again, infants spent more time in nipple contact in dry season than wet season and at this age also spent less time feeding independently in dry season than in wet season. However, there was very little variation in independent locomotion in dry and wet seasons at this age.

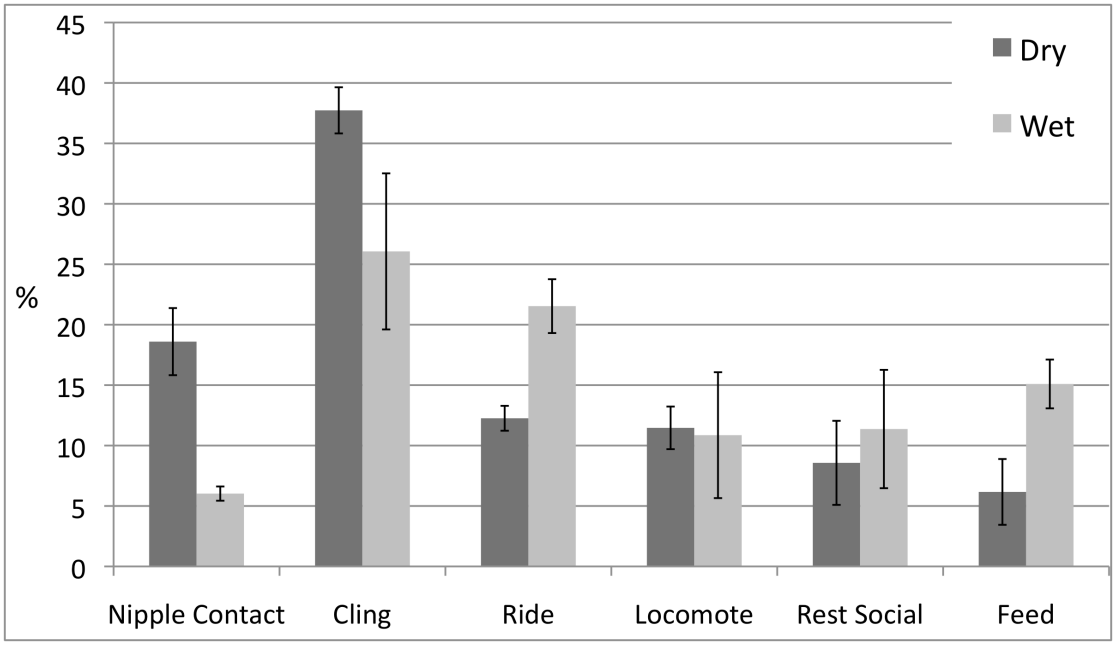

Fig. 03.08. Activity budgets for 4 individuls aged 5 - 7 months during the wet and dry seasons (N = 4). Bars indicate mean ± standard deviation.

Comparison of Populations

Nursing

With the exception of one study of olive baboons (Nicolson 1982) observations of other populations were stopped before nursing had ceased completely. Thus, it seems that Kwano baboons continued to nurse for approximately 20 weeks later than this population (Fig. 03.09). However, Kwano baboons spent a lower percentage of time nursing earlier in life. This lower rate was most pronounced in the first 10 weeks of life, while it approached the rates of infants in other study groups after this stage (cf. Fig 03.09). Fewer data are available for older infants; however, three out of four infants studied in the oldest age group of 70-95 weeks in the current study were observed to nurse. Nursing accounted for almost 5% of mother-infant interactions between the ages of 80-95 weeks.

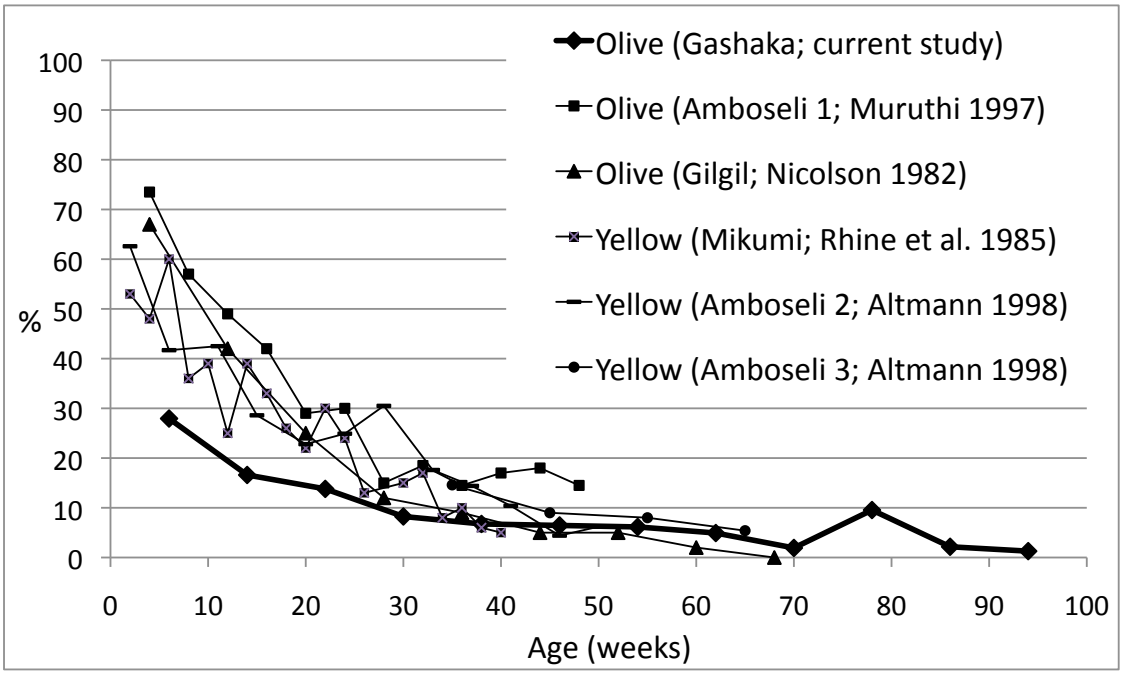

Fig 03.09. Time spent nursing. Data from 6 baboon populations, with the current study highlighted (adapted from Roberts 2011). The data collection cut off is not known for all studies, however for the Amboseli 1, Amboseli 2 and Mikumi populations, data collection ceased by 12 months of age or before.

Contact Time

The time Kwano infants spent in contact with their mothers shows a similar pattern of variation with age as other populations, though contact time was slightly lower at younger ages, and contact is maintained at appreciable rates for longer (Fig. 03.10).

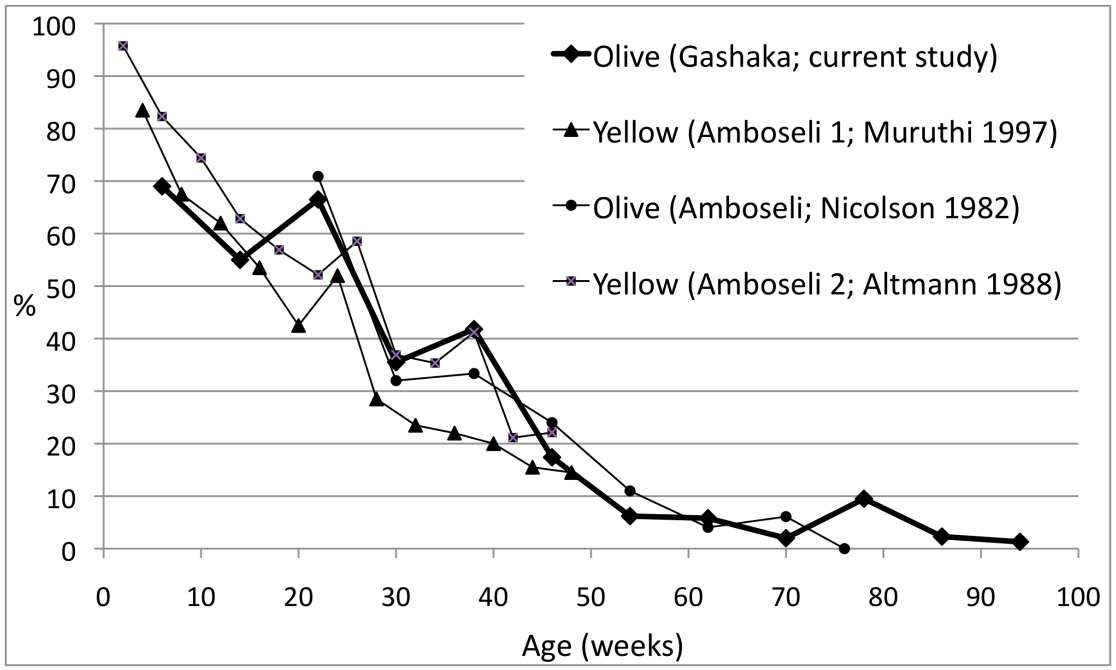

Fig 03.10. Time spent in contact with mother. Data from 4 baboon populations, with the current study highlighted (adapted from Roberts 2011). For Amboseli 1 and Amboseli 2 populations, data collection ceased by 12 months of age or before.

Adult and Sub-adult Activity Budgets

A total of 215.8 h of observations were made of seven focal animals, by JT (Tab. 03.03). However, in order to make a more valid comparison with infant activity budgets, only data recorded between the same hours as infant focal follows were included in the following analyses. Thus, 160.7 h of observations made of seven individuals are included in the following analyses. A breakdown

of adult and sub-adult activity (Fig. 03.11) showed that 45.1% of their time was spent feeding. Other major activities observed were locomotion, resting and grooming. States that did not fit into prior categorisation, commonly social interaction including copulation and aggression, accounted for less than 1% of activity.

Tab. 03.03. Observation time (h) for adult and sub-adult focal animals from 0600-1200 (for all group demographics, see chapter 2).

	Hour						
Individual	0600-0700	0700-0800	0800-0900	0900-1000	1000-1100	1100-1200	Total
AMY*	2.6	4.5	4.6	4.3	4.1	3.3	23.4
ANN*	2.6	4.7	4.5	4.2	4.1	3.3	23.4
MUR	1.9	4.4	4.7	4.5	3.8	3.4	22.7
TAL*	2.3	4.3	4.5	4.2	3.9	3.3	22.5
DRK	2.5	4.2	4.3	4.6	3.2	3.2	22.0
LDI	2.4	4.5	4.7	4.5	4.0	4.0	24.1
LMI	2.3	4.6	4.7	4.5	4.0	4.0	24.1
Total	16.6	31.2	32	30.8	27.1	24.5	

*subadult

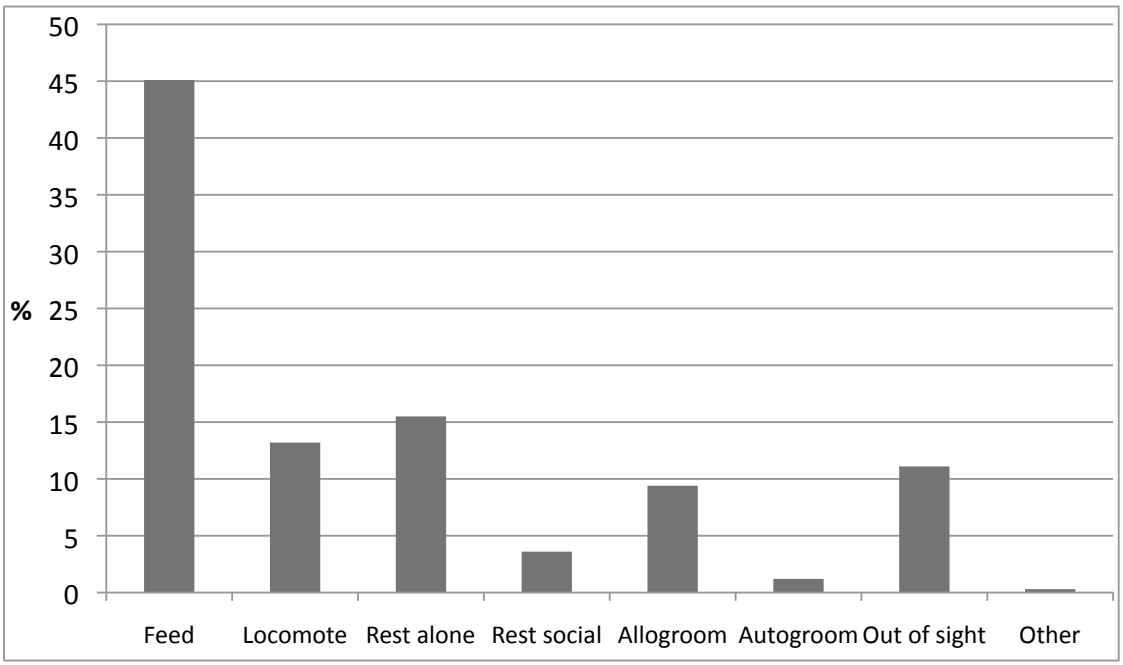

Fig. 03.11. Mean time spent engaged in the most common activities (%) for all focal adults and sub-adults (N = 7), from 0600-1200.

DISCUSSION

In describing the changes in activity budgets as infants age, one main objective was to quantify the ages at which major changes in nursing activity took place, signalling the onset of weaning (Martin 1984, Lee 1996). Here, the percentage of time spent in nipple contact, used as a proxy for nursing, becomes smaller than the percentage of time spent feeding independently at 7-9 months of age. Nipple contact becomes less common again at 10-12 months, before being maintained at a steady rate until 21 months (cf. Fig. 03.03).

Further objectives were to present a comparison with adult behaviour at Kwano, and a further comparison with infant behaviour at other study sites. Overall, data show the expected increase in independence as infants age, which generally follows the same pattern as that of other studied populations. However, while infants in the Kwano group are more dependent on their mothers for locomotion, the percentage of time spent nursing, while it declines with age, seems consistently lower than that observed in other groups (cf. Fig 03.10). Firstly it is important to note that this trend must be treated with caution as studies of other populations are not directly comparable due to differing data collection protocols. Secondly, the trend seems somewhat paradoxical since it was predicted that the environmental conditions at Kwano would favour increased investment from mothers, manifested by both feeding and carrying their infants more than other groups. However, this may be explained by differences in activity budgets in wet and dry seasons, with dry season being associated with more maternal investment, and wet season associated with less maternal investment.

Generally, while the relationship between age and various activities is frequently not linear, often it appears to be the 19-21 month age category that contradicts the general trends. For example, the amount of time spent engaged in independent feeding generally increased with age as expected, yet decreased in the 19-21 month age class, while nipple contact increased during this age class after decreasing until that point. These unexpected results may be due to two issues with the data available for this age class – overall, fewer data are available, and within those data, one individual contributed a disproportionately large number of the observations. Moreover, this is the individual that showed high levels of nipple contact at this age, which could for example account for the decrease in the average percentage of time spent feeding independently for all individuals grouped (cf. Fig. 03.03).

Contact and Independence

While patterns of change in activity generally followed that of other populations, both contact and nursing continued for longer in the Kwano group. Nursing was observed up to 20 weeks later than at other study sites, and three out of four infants observed during 19-22 months of age were seen to nurse intermittently at this age, although one individual accounted for a large proportion of observations of nursing after 19 months (cf. Tab. 03.02). Since it was not possible to carry out inferential statistics to compare these data with other populations, this does not constitute evidence that weaning is delayed at Kwano, though it is consistent with such a hypothesis.

With regard to the amount of time infants spent being carried by their mother, these patterns might reflect the fact that the group travels more in dry season due to the decrease in the availability of water and certain foods such as fruit

(Wahungu 1998). The increase in the home range of Kwano group in dry season, from 0.87km^2 to 1.36km^2 (Warren 2003) would make young infants more dependent on their mothers for transport during this time (Fig. 03.02). It seems the initial description of the site was flawed in that it is not sufficient to classify the environment as simply having high abundance of food (chapter 3); when considering infant behaviour, the type of food available is crucial. Flower blossoms, low hanging fruit and berries, and green grass shoots have all been identified as good weaning foods, i.e. they are easy to obtain from the ground and easy to digest (Altmann 1980). These are foods that are not available in the dry season (Warren 2003). Correspondingly, when only lower quality food is available, infants require more milk to supplement their diets, and this is true both during the first 3 months of life (cf. Fig. 03.07) and at the onset of weaning (months 5-7; cf. Fig. 03.08). If suitable weaning foods are not available, the weaning process might begin later or progress more gradually.

In addition to the seasonal affects on food availability and group movement, parasite loads may be a factor when considering infant behaviour in this group. Parasite diversity is high in Kwano infants, significantly exceeding levels found in all other age groups (Boulton 2010). For this reason, young infants walking rather than being carried in the wet season may be exposed to unnecessary risk. Correspondingly, the percentage of time spent locomoting as opposed to being carried was much lower in infants aged up to 3 months in the wet season. Again, while consistent with such hypotheses, data do not constitute evidence that development is delayed in Kwano group as it was not possible to carry out inferrential statistics when comparing data between wet and dry seasons, or across different populations.

Rest

The unexpected patterns shown in the amount of time spent resting alone or socially (cf. Fig. 03.05) may be an artefact of the uneven distribution in observation time across age groups (cf. Tab. 03.02). Data shown are based on counts, with observation time fluctuating makedly between different age groups, and potentially causing unexpected fluctuations in counts. Such effects may be compounded by the fact that rest constitutes a relatively small proportion of infant activity budgets, potentially more susceptible to fluctuation. Consequently, it is not possible to determine the implications of the significant GLMM for rest, as the relationship is non-linear, and one cannot claim for example, that resting alone always increases with age when the average percentage of observations of rest does not. However, as one might expect, very young infants spent almost no time resting alone. This is important when considering the development of vocalisations associated with being separated from the group (chapter 5).

Grooming

Generally, the amount of time spent grooming increased with age with the exception of the 19-21 month age class, where there was a notable decrease in time spent grooming. As mentioned previously, the unexpected decrease in grooming at ages 19-21 may be a reflection of the behaviour of one individual from whom the majority of observations in this age group were made, since that individual appeared to spend a lot of time in nipple contact with her mother and thus less time engaged in other activities at this age.

In adults baboons, as well as serving to remove parasites, grooming forms an

important social function that maintains group bonds, and is linked to coalition formation (e.g. Saunders and Hausfater 1988; Barrett and Henzi 1999). Therefore, it is to be expected that grooming makes up a very small percentage of an infant's activity budget, since complex interactions such as coalition formation will not be a factor at this age. Here, the data from the current study may be affected by a gender bias in the sample – 7 of the 9 infants for whom activity budgets are available were male, and the role of grooming has been particularly highlighted in adult females (Barrett and Henzi 1999). The role of grooming in social interactions between adult females will be revisited in relation to infant handling (Chapter 4). Adult females in Kwano troop spent 10.0% of their time grooming or being groomed (cf. Fig. 03.11; Thompson 2012), so the low percentage of time infants spent allogrooming could be an affect of age, rather than specific to this group. Moreover, the decrease in grooming at 19-21 months may reflect a lower observation time in this age category than some others, or the fact that two males and only one female were observed at this age. Since grooming is an important factor when forming social bonds in adult females (Silk et al. 2006) this may reflect sex differences, as the sample of infants included in the current study comprises 7 males and 2 females. A more valid comparison may be with activity budgets of adult males, but these data are not currently available for baboons at Kwano.

To summarise, the environmental conditions, including food availability, seasonality and parasite loads, may lead to delayed ontogeny in Kwano infants. While limited due to the difficulty of comparing results from studies using differring data collection protocols (resulting in only one direct comparison study from another site, with an unpublished N), if confirmed, this

finding could explain the unusually long inter-birth intervals observed at Kwano (Higham et al. 2009). Since the three infants observed between 20-22 months of age required supplementary milk at up to 21 months of age, their mothers must invest heavily in each infant before being able to conceive another.

CHAPTER 04:

INFANT HANDLING: TESTING THE BIOLOGICAL MARKET THEORY

Sub-adult Murna pulls 1 month old infant Emma as he approaches his mother, Ymke. Photo: Suzanne Harvey, 2010.

INTRODUCTION

Handling of infants by non-mothers is common across primate species, often involving an adult female removing another female's infant to interact with it physically. Infant handling ranges from brief touching, grabbing or pulling to allo-mothering, in which a handler cares for the infant for a prolonged period of time (McKenna 1979; Reidman 1982; Fairbanks 1990). In baboons, infant handling ranges from benign muzzle contact to aggressive grabbing and pulling (e.g. Silk et al. 2001). Baboon mothers are very possessive, and reluctant to hand over their infants, such that handling attempts are often unsuccessful while actual handling is often very brief. In rare cases, infants are kept from their mothers for prolonged periods of time ('kidnapped'), until they become dehydrated and weakened (Hrdy 1976; Shopland and Altmann 1986). In addition to the potential for physical harm to infants, handlers can cause considerable stress to mothers in their efforts to avoid handlers, to resist handling attempts, and to respond to aggressive handlers (Altmann 1980; Maestripieri 1994). This suggests that infant handling in baboons is a behaviour that is costly to both the infant and the mother.

Numerous hypotheses have sought to explain infant handling – and in particular extensive allo-mothering - in primates (14 theories reviewed by Maestripieri 1994). During allo-mothering, mothers voluntarily hand over their infants to non mothers, who care for them for a prolonged period of time. Therefore, the majority of theories of infant handling (Maestripieri 1994) focus on mutual benefits for both the handler (e.g. learning mothering skills) and the mother (e.g. relief from caregiving). Such hypotheses are relevant for species in which allo-mothering is common, but they are less applicable to baboons.

Here, allo-mothering is not observed, and infant handling has thus been more convincingly explained as a functionless bi-product of selection for maternal care (Silk 1999), an evolved product of female reproductive competition (Wasser and Barash 1983; Maestripieri 1999; Kleindorfer and Wasser 2004), or the result of a biological market in which females trade infant handling for grooming (Henzi and Barrrett 2002).

The Cost of Handling

The relative costs of infant handling behaviour must be considered for all participants – mother, infant and handler – before predictions can be made regarding the presence of a market for infants, and its potential affect on those infants. In the discussion of costs, the type of handling behaviour displayed in a group is of vital importance. For example, while increased aggression against potential handlers has been observed in rhesus macaques (Troisi et al. 1988) in the same group, positive handling and allo-mothering behaviour met with little resistance from mothers (Schino et al. 2003). Moreover, aggression towards infants from handlers increased when infants produced distress vocalisations (Jovanovic and Gouzoules 2001). Thus, this is an example of a group in which there are potentially high costs for all participants, but also potential benefits due to handling bouts lasting up to 20 minutes (Schino et al. 2003), thus providing relief from caregiving for the mother. In the case of baboons, where handling is of short duration and can be aggressive (Altmann 1980, Silk et al. 2001) this potential benefit is absent. Therefore, it seems likely that theories that define handling as a selfish behaviour that only benefits the handler seem most applicable (McKenna 1979).

If handling is to be considered as a selfish behaviour that benefits only

handlers, this raises the issue of power differentials between mother and handler, and indeed, the way in which infant handling takes place has been shown to vary according to the relative rank of mothers and handlers (Henzi and Barrett 2002). This is expected to be a key consideration in the current study, due to the strict linear dominance hierarchy of olive baboons (Smuts 1985). Consequently, due to the potentially high costs of 'trading' an infant when no allo-mothering takes place, market value theory is not expected to be applicable to the study group, and two alternative 'selfish' theories will be discussed as possible alternative explanations.

Bi-product of Maternal Motivation

The bi-product hypothesis states that infant handling behaviour can be explained as a functionless bi-product of selection for maternal care, as individuals who show higher rate of responsiveness to infants are likely to make better mothers (Silk 1999). This theory is supported by the fact that, despite the widely differing nature of infant handling, female primates across species appear to experience strong attraction to neonates (Hrdy 1976; Paul 1999). This increases the rate of approaches to mothers with infants (Silk et al. 2003). It has been argued that aggressive forms of infant handling do not necessarily contradict this hypothesis, since it could be a bi-product of general protectiveness, rather than a motivation to harm infants (Maestripieri 2011).

Female Reproductive Competition

A second hypothesis sees infant handling as a reflection of female-female reproductive competition (Wasser and Barash 1983; Blaffer-Hrdy 1999). If handling is costly in terms of reducing the reproductive success of the mother

it will reduce the number of offspring that will be competing with the handler's own current and future infants. The extreme end of this motivation is infanticide, which is more typically seen as part of male reproductive strategies, but has also been reported in female primates (e.g. Townsend et al. 2007). The hypothesis is supported by the fact that the frequency of aggressive handling, such as grabbing and pulling, is a significant predictor of infant mortality in yellow baboons (Kleindorfer and Wasser 2004).

Biological Market Theory

This concept was initially developed to explain mate choice and seemingly illogical altruistic behaviours (Noë and Hammerstein 1994). For example, in pied kingfishers, males sometimes feed unrelated infants. This behaviour increases the chances of the female mating with the male that provides the most food for her infants (Reyer 1984), or, in market terms, the 'highest bidder'. The logic of a biological market is that individuals form two trader classes, and are either 'sellers' (offering a commodity) or 'buyers' (bidding for the commodity). A major tenet of biological market theory is that different commodities are traded for the mutual benefit of the buyer and seller. In the case of the kingfisher, the female's tradable commodity is the male's future mating access, for which males will bid by providing food for her infants. While each male derives no direct benefit from feeding unrelated infants, they are bidding for the mother to 'trade' with them, by exchanging mating for food.

The same logic has more recently been applied to infant handling in baboons (Henzi and Barrett 2002). Here, it has been argued that infants are the desirable commodity, that the mother is the seller of this commodity, and that

other females bid for access to her infant by providing grooming. The initial finding supported two main predictions of biological market theory: grooming led to infant handling (the price paid), and grooming bout length increased when fewer infants were available (each had a higher value). Furthermore, high ranking females received longer grooming bouts before handling took place, seen as an indicator that these individuals are able to demand a higher price. These findings form the basis of market value theory in relation to infant handling.

Since this initial application of biological market theory to baboons, there have been mixed results for other primate species. In long-tailed macaques (*Macaca fascicularis*), vervet monkeys (*Chlorocebus aethiops*) and sooty mangabeys (*Cercocebus atys*), grooming led to infant handling and infant supply was related to grooming duration (Gumert 2009; Fruteau et al. 2011). In tufted capuchins (*Cebus apella*), grooming led to infant handling, but infant supply was not related to how long handlers groomed mothers (Tiddi et al. 2010). In spider monkeys (*Ateles geoffroyi*), embraces rather than grooming became more common when females had young infants, but simpler explanations, such as signalling benign intent, were equally consistent with the data (Slater et al. 2007). In olive baboons (*Papio anubis*) in Kenya, mothers were groomed longer than other females. However, grooming was not related to infant availability but to the relative grooming activity of the mothers. There was no clear evidence for a biological market (Frank and Silk 2009). Moreover, there is no a priori reason to assume that the dynamics of infant handling can only be assessed by rates of grooming. Communication signals are known to be associated with this behaviour, and may affect the relationship between

grooming and handling.

Communication Associated with Infant Handling

In baboons, infant handling is often associated with vocal behaviour, particularly grunting. Thus, mothers with infants are often approached by handlers who are grunting. Such 'infant grunts' are acoustically different from grunts produced in other contexts, such as those given during group movements (Rendall et al. 1998; Owren et al. 1997). In playback experiments, different grunt variants produced different responses in recipients (Owren at al. 2002), demonstrating that baboons discriminate grunt variants and associated behavioural context. The suggested function of 'infant' grunts is a more general motivation of dominant animals to signal benign intent to subordinates, regardless of whether infants are present (Cheney and Seyfarth 2007; Slater et al. 2007). Adult baboons have been shown to alter grunting rates and duration depending upon both environmental conditions and context (Ey et al. 2009).

For a market to be sustainable, there must be mutual benefit for both parties in the interaction. We therefore aim to test the biological market theory of infant handling in a primate in which allo-mothering is not present, and mothers do not benefit from allowing other adults to handle their infants. In this study, we re-examine the idea that infant handling in baboons can be explained with biological market theory, i.e. that buyers compete for a desirable commodity (infants) whose availability is controlled by sellers (mothers). The predictions of biological market theory are as follows: (a) mothers are more likely to allow handling when grooming occurs; (b) grooming bout length increases when

fewer infants are available, as each infant has a higher value; (c) grooming is less likely to be reciprocated by mothers than non-mothers; (d) handlers who are also mothers are more likely to attempt to handle an infant without grooming its mother compared to handlers who are non-mothers; and (e) differences between the rank of mothers and handlers will affect the occurrence and duration of grooming.

However, due to the absence of allo-mothering, potential for aggressive handling, and lack of potential benefits for the mother and infant, grooming is not expected to buy access to infants in the current study group. The finding that mothers are less likely to reciprocate grooming has been explained without the need for a biological market, and may simply reflect greater constraints on mothers' time when nursing an infant (Frank and Silk 2009). Therefore, this may also be the case for mothers at Kwano, but would not comprise evidence for a biological market. With power differentials and relative rank expected to be important in a selfish behaviour, differences in handling behaviour depending on rank are expected. In line with the current study's objectives of documenting socialisation, handling of infants of all ages will be considered, to describe how infants become less passive and more independent during infant handling interactions.

MATERIALS AND METHODS

Analyses followed Henzi and Barrett (2002). For this reason, firstly, only infants in the 0-3 month age range were included, for whom approximately 200 hours of observations are available. The 0-3 month category was chosen primarily to enable a comparison of the data presented here with those on which the market value theory of infant handling was founded, but additionally

from a theoretical point of view, since the changing colour of the natal coat in older infants may prove an unintended confound. Infants aged 0-3 months appear similar in size and colour, and thus should be equally attractive to handlers before testable variables such as rank are considered.

Data Collection

From March-June 2010 and October 2010-April 2011, focal infants were followed from 0600-1200 hours on each observation day, resulting in a total of 411 hours of observations. Grooming interactions between adults within 5 m of the focal animal were noted ad libitum. Grooming bout length was recorded in minutes, i.e. if grooming was still ongoing at the time of the next instantaneous on-the-minute sample, another minute was added to the duration. A bout was deemed reciprocated if groomer and groomee switched roles and another bout was initiated in the same or following minute. Infant handling was likewise recorded ad libitum, and the identity of the handler, type of handling behaviour (e.g. grab, pull), number of grunts produced and outcome (e.g. mother resists, handler grooms mother) were recorded.

Analyses

The primary aim of this chapter was to replicate the study carried out by Henzi and Barrett (2002) in which the market value hypothesis was originally proposed. Therefore, the data analyses used by Henzi and Barrett (2002) are replicated as closely as possible. Where differing data collection protocols do not allow for an exact replication, this is stated. This method requires considerable reduction of the dataset, described in detail below, in an attempt to prevent inflation of N due to multiple sampling of the same mother-handler

grooming dyads (Barrett et al. 1999, 2000, Henzi and Barrett 2002).

To further enable comparisons with the existing literature, analyses focussed on adult female handlers only. Of all handling bouts (*N* = 689), adult female handlers accounted for 72.3%, juvenile females 22.9%, adult males 3.0% and juvenile males 1.7%. As per Henzi and Barrett (2002) two separate databases were used: the grooming database, and the infant handling database. This results in different values of N for different analyses, therefore N is reported for each set of analyses, as well as the database data were taken from.

Following the original method, "to avoid over-representation of particular mother– handler dyads, we … took all the handling episodes for each mother and partitioned them according to infant age. Then, for each month of life, we extracted randomly one handling episode for each female with whom the mother interacted during that period" (Henzi and Barrett 2002, p.917). Therefore, in the infant handling database, all handling incidents were grouped according to infant age (0-3 months) to further control for attractiveness, i.e. the differing appearance of the natal coat (detail chapter 2). There were four mothers, each of whom had a potential of 10 handlers (N =11 adult females in the group), giving a maximum of 40 possible dyads. In reality, not all potential handlers attempted to handle all infants, and 30 different dyads were observed. This always remains constant. For example, Momi, a mother, was part of 5 dyads, of which 44 events were observed. One random event was selected from each of these dyads using a random number generator, per infant's month of life. This method yielded a total of 36 handling bouts for all individuals: 6 with grooming, and 30 without grooming.

In the grooming database, one grooming bout was selected, using a random number generator, from each female (*N* = 11) from each grooming dyad. As per the infant handling database, the total number of observed dyads did not equal the total number of possible possible dyads, since not all females groomed every other female in the group. For example, Ladi was part of 7 grooming dyads, of which there were a total of 22 events. One random event was selected using a random number generator for each dyad. This controls for differences in grooming activities across dyads (Barrett et al. 1999). This process yielded 53 infant related (IR) grooming bouts, and 13 non-infant related (NIR) grooming bouts. This bias emerged because infants served as focal animals. NIR bouts were defined as no infant within 1 m of the grooming interaction. IR bouts included instances where an infant was merely present, as well as cases where handling took place.

For both grooming and infant handling events, this process severely reduces the available data. However, the selection of a random dataset, however small, is important because it avoids issues of pseudo-replication (Barrett 1999, Waller et al. 2013). Moreover, from a theoretical point of view, “it is justified since … our predictions apply to any single grooming bout” (Henzi and Barrett 2002, p.917). Despite these considerations being taken into account in the method replicated here, some pseudo-replication issues remain, since the infant handling database includes more than one data point per individual due to the partition of events by infant age. Therefore, any interpretations of these results are limited except for direct comparisons with the original study. Since the Market Value Theory was initially proposed (Henzi & Barret 2002), more sophisticated statistical methods have become available, enabling alternative

analyses of the effects of key variables such as grooming and rank differences on infant handling behaviour. Rather than reducing the size of the dataset to avoid pseudo-replication, random effects models such as Generalised Linear Mixed Models (GLMMs) can account for dependence between observations (Millar and Anderson 2004). In terms of the current study, this allows for the variable 'individual identity' to be incorporated into the linear predictor of a generalised linear model as a random effect (Mcculloch and Neuhaus 2013); i.e. the dependence between multiple handling events involving the same infant can be accounted for when modelling which variables affect handling type. For this reason, a GLMM has also been carried out, in addition to the replication of the original analyses.

Infant handling was divided into four types (definitions adapted from Henzi and Barrett 2002), in which the handler (a) removed the infant from contact with its mother to inspect and manipulate it, (b) touched and manipulated the infant while it remained in contact with the mother, (c) touched the infant and then tried to remove it from the mother, who resisted strongly and kept the infant in contact, and (d) communicated to the mother and infant by grunting and/or lip-smacking, nuzzling or embracing the infant, while it remained in contact with the mother.

To investigate the association between grooming and handling, handling bouts were categorized initially as grooming followed by handling, and handling followed by grooming. A further bout type, not used by Henzi and Barrett (2002) was added: grooming before and after handling. The remaining bouts were classified as handling without grooming.

To investigate the effect of dominance on infant handling, rank distance was calculated as a continuous variable, comprising the rank of the handler minus the rank of the mother (range: -7 to +8). A further binary variable of rank, higher or lower, was then calculated from these positive (higher) and negative (lower) values.

RESULTS

Characteristics of Handling

Analyses of the entire infant handling database for 0-3 months of age (*N* = 490 events), showed that grabbing accounted for 59.4% of handling attempts (Fig. 04.01). This was defined as grabbing the infant without pulling or forcibly trying to remove it from the mother, and also includes grabbing and holding on to the infant without pulling. Cases in which the handler did pull the infant but did not remove it from the mother accounted for 20.2%, and muzzle contact or embracing accounted for 14.3%. Handlers only removed the infant from its mother in 0.6% of cases, and in all three of these incidents the handler subsequently either dropped or threw the infant to the ground, and did not appear to have any interest in possessing it. The remaining 5.5% of cases involved lipsmacking or reaching out to the infant without making contact, and while these behaviours were clearly directed at the infant, since no contact was made they were not included in the following handling analyses. No allo-mothering was observed.

Fig. 04.01. Examples of infant handling in Kwano group. An unidentified handler pulls Eto'o from his mother Sadiya (top). Murna grabs Eggi from his mother Rabi (bottom). (Photographs: Suzanne Harvey, 2011 and 2010.)

Trading Grooming for Handling?

For a random set of events from the grooming database in which infant handling occurred (N = 21; note this is not IR grooming when infants are within 1m, but only occasions when handling occurred), grooming occurred after handling in 57.1% of cases, never before handling, and both before and after handling in 42.9%. The first prediction of the market theory, i.e. that maternal responses to handling attempts were dependent upon whether grooming occurred prior to handling, was therefore not supported. Similarly, bout duration did not vary according to handling type (N = 21 randomly selected events, Kruskal-Wallis ANOVA: X^2 = 4.214, P = 0.318), suggesting that handlers do not offer more grooming after forcibly trying to remove an infant than after merely greeting or nuzzling it.

Outcomes of handling were not always available since some infant handling events were recorded ad libitum, but for those events in which these data were available (N = 29 randomly selected events), 57.2% of handling bouts ended with a handler resting next to the mother and infant without grooming, 21.4% with grooming the mother, while 17.9% of handling was followed by a handler leaving the mother and infant, and 10.7% with the mother actively avoiding or resisting the handler. Excluding cases in which the handler determined the outcome by leaving or grooming the mother after handling, mothers were not more likely to passively tolerate the handler than to move away and avoid her than chance (binomial (0.5) p = 0.34, 2-sided).

Reciprocation and Duration of Grooming Bouts

Using the grooming dataset, IR bouts (N = 53) were significantly more likely to

be non-reciprocated than NIR bouts (*N* = 13): IR non-reciprocated, 96.0%; reciprocated, 4.0%; NIR: non-reciprocated 69.0%, reciprocated 31.0% (2-tailed Fisher's Exact test: *P* = 0.012.) A 2-way ANOVA showed that both bout type (IR vs. NIR) and whether the bout was reciprocated, significantly influenced grooming bout length (bout type: *F* = 7.99, *P* = 0.006; reciprocation: *F* = 40.99, *P* = <0.001). There was also a significant interaction between bout type and reciprocation (*F* = 12.21, *P* = 0.001). Non-reciprocated bouts tended to be shorter, with little difference between bout types and high variation, whereas reciprocated bouts tended to be longer, particularly in the case of IR bouts (mean ± SD; non-reciprocated bouts: IR 2.04 ± 1.98min, NIR 2.78 ± 1.99min, reciprocated bouts: IR 13.00 ± 7.07min, NIR 6.00 ± 4.76min, *N* = 66 randomly selected dyads; comprising 53 IR and 13 NIR). Therefore the presence of an infant did affect bout length and the likelihood of reciprocation, despite the fact that maternal responses to handling attempts were not affected by the occurrence of grooming.

The infant handling dataset showed that there was no effect of dyad type on the likelihood that grooming occurred (*N* = 36 bouts; mother-mother: without grooming 79.0%, with grooming 21.0%; mother-non mother: without grooming 82.0%, with grooming 18.0%; Fisher's Exact Test: X^2 = 0.058, *P* = 1.00). Mothers were not more likely to handle infants with than without grooming.

Dominance Effects on Grooming and Grunting

Having found no relationship between maternal responses to handling and the occurrence of grooming, the next set of analyses investigated the influence of the handler and mother's dominance on the occurrence of either grooming or

communication signals associated with handling. Events where grunting did and did not occur were not associated with different rank distances (-8 to +9) between the interactants (With grunts: N = 17, median = 3, IQR = 4; without grunts N = 19, median = -1, IQR = 7; Mann-Whitney U test: Z = -1.242, P = 0.214). However, events where grooming did and did not occur were significantly associated with different rank distances (-8 to +9) between the interactants (With grooming: N = 8, median = 4, IQR = 7; without grooming: N = 28, median = 1.5, IQR = 7; Mann-Whitney U test: Z = 2.289, P = 0.022).

There were some additional patterns in the data (Fig. 04.02). First, the number of cases of handling (a) without accompanying behaviour, (b) with grunting only, and (c) with grunting and grooming were close to identical in terms of rank relations (neither: lower ranking: N = 7, higher ranking: N = 6; grunting only: lower ranking: N = 8, higher ranking: N = 8, grooming and grunting: lower ranking: N = 0, higher ranking N = 1). This was in contrast to cases of handling with grooming only, which were heavily biased towards lower-ranking individuals (lower ranking: N = 6, higher ranking: N = 0), i.e. it only occurred when mothers outranked handlers.

In the next set of analyses, the grooming dataset was partitioned into cases where the handler was either higher- or lower-ranking than the mother, to control for dominance effects on handling interactions. There was no effect of infant availability on grooming bout length for lower-ranking handlers (Kruskall Wallis: N = 33, X2 = 1.79, df = 2, P = 0.407). There was a significant effect of infant availability on grooming bout length for higher-ranking handlers (Kruskall-Wallis: N = 33, X2 = 6.39, df = 2, p = 0.041). However, pairwise comparisons revealed that the only significant difference was between zero

and two other infants in the group (p = 0.038) with the difference in grooming bout length when one or two infants were present (p = 0.284) and when one or zero infants were present (p = 1.00) both non significant. Therefore, the second main prediction of market theory, that infant availability would influence grooming bout length, has little support.

After cases were divided according to whether the handler was higher or lower ranking than the mother, neither category showed a significant relationship between handling type and the occurrence of grooming or grunting (lower ranking handler: X^2 = 1.298, P = 0.433; higher ranking Fisher's Exact test: X^2 = 1.951, P = 1.00), though attempts to forcibly remove infants only occurred when handlers outranked mothers (cf. Fig. 04.02).

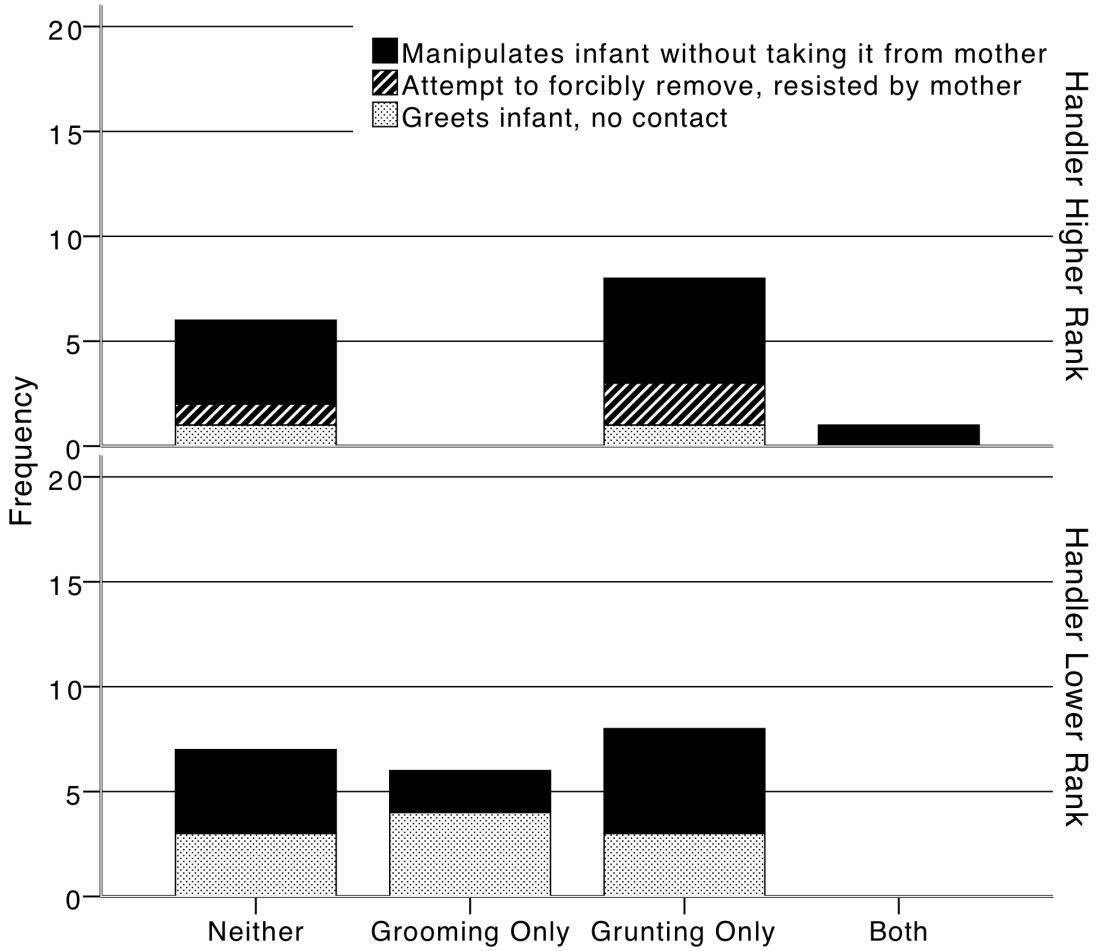

Fig. 04.02. Variation in the frequency of each handling type, in relation to the occurrence of grooming and grunting, for higher (N = 15) and lower (N = 21) ranking handlers. Data presented are random selected events for infants aged 0-3 months.

Observations of Atypical Handling

The following observations describe atypical handling bouts that, while not frequent enough for systematic analysis, might give additional insight into the functional significance of infant handling in olive baboons.

(a) While allo-mothering was not observed in this group, one incident of adoption was. An adult female somehow obtained an infant from another

group while being pregnant. The infant's biological mother was never seen. She nursed her adopted infant for approximately one week before it became weak and eventually died (N. Alberts, pers. comm.). Shortly afterwards, the female suffered a miscarriage.

(b) One mother's infant died approximately 2 days after birth. The dead infant continued to attract attention of other females, while the mother continued to carry it, despite the absence of movement or other behaviour, such as vocal cues or nursing that might act as signals of the presence of an infant to handlers.

(c) The highest ranking female (whose own infant was 12 months old) was seen to repeatedly remove a middle-ranking mother's nipple from the mouth of her young infant throughout an entire observation day.

What Happens to Older Infants?

While the majority of all observations of infant handling were directed towards infants aged 0-3 months (0-3 months: total N = 506, 4-22 months: total N = 382) handling did continue at older ages (Fig.04.03). As the age cut-off was designed to control for the appearance of infants as a proxy for attractiveness, the analyses presented here describe the characteristics of handling in infants aged 4-22 months and the effects of dominance on this behaviour, and do not test all the hypotheses of the market value theory.

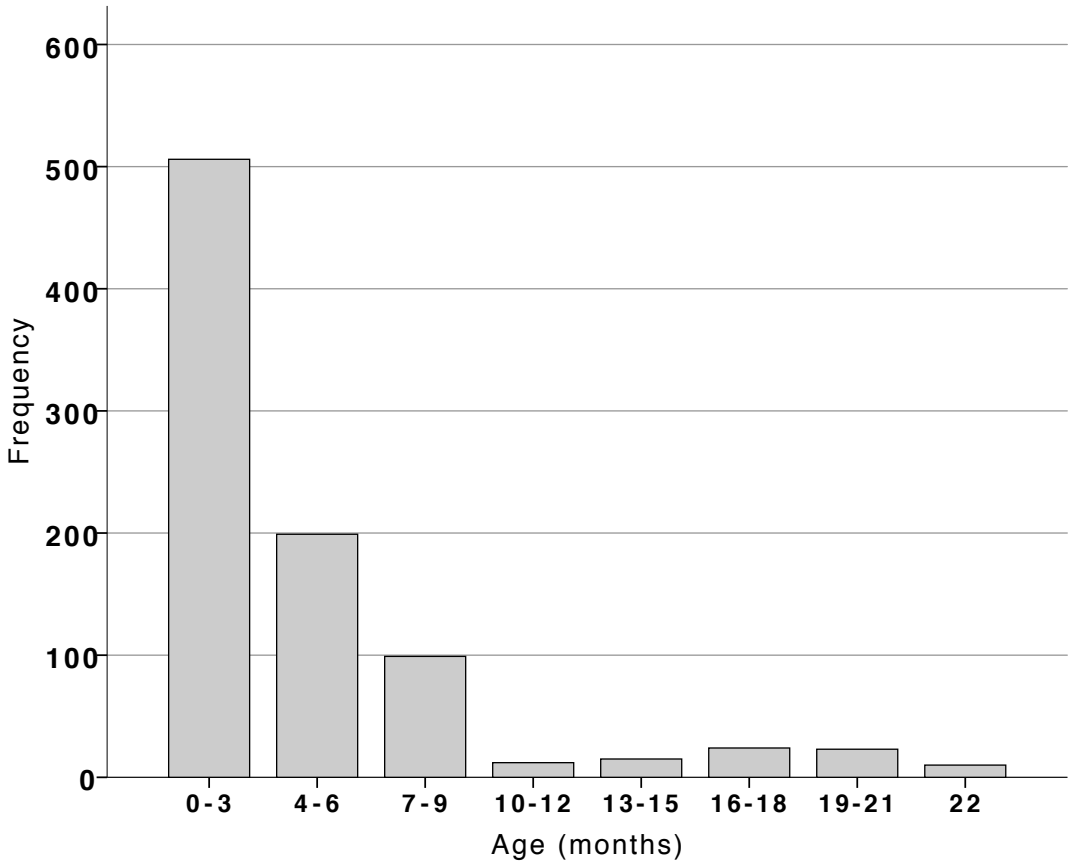

Fig.04.03. Frequency of handling for all age groups. Frequencies are for the total number of handling attempts, and thus represent repeated handling of the same infants.

Again, the preparation of data largely followed that of Henzi and Barrett (2002) in that data were first partitioned by ages, then a random case was selected for each dyad, for each month of life, to enable comparison of handling behaviour directed at all ages of infants (detail in methods). It was not possible to analyse the effects of the number of infants in the group, since there is nothing obvious in their appearance at older ages that defines infants; when not nursing at 20 months old, an infant's appears almost indistinguishable from a juvenile, and indeed some are weaned by this age. Correspondingly, the mother of this infant may still be lactating, but it is not possible to know whether another adult

would class her as a mother with no obviously dependent infant present, therefore it was not possible to compare mother-mother and mother-non mother dyads for older infants. Consequently, analyses of handling of older infants are restricted to the type of handling, the occurrence of grooming and grunting, and effects of rank on these behaviours.

The number of events is much higher than the 0-3 month age group due to the increased age range rather than a higher rate of handling. Additionally, data are available for more individuals in the 4-22 month age group than the 0-3 month age group, and therefore the same method used for younger infants – grouping incidents first according to infant age, then extracting one random example for each mother-handler dyad per month of life – yielded a larger dataset. In this section, data are grouped into 3 month categories and presented for the entire duration of infancy from four months of age.

Characteristics of Handling

For a random set of events (N = 125) the most common form of handling was grabbing without forcibly removing infants from their mothers, which accounted for 55.2% of handling attempts. Cases in which handlers pulled an infant and tried to remove it from its mother accounted for 24.0% of handling attempts, and in 20.8% of cases, handlers greeted an infant with muzzle contact or embracing. From the randomly selected events, there were no cases in which handlers successfully removed an infant from its mother, although these accounted for 2.6% of all observations in this age group, so this behaviour was not entirely absent but was very rare (handling type per 3 month age group, Tab. 04.01, 04.02). No allo-mothering was observed.

Tab. 04.01. Type of Handling of infants aged 4-22 months, for randomly selected events (N = 125).

		Handling Type			
Age (months)	Total N	Removes from mother and handles	Manipulates infant without taking it from mother	Attempt to forcibly remove, resisted by mother	Greets infant, no contact
4-6	47	0	25 (53.2%)	8 (17%)	14 (29.8%)
7-9	33	0	22 (66.7%)	7 (21.2%)	4 (12.1%)
10-12	10	0	3 (30.0%)	0	7 (70.0%)
13-15	6	0	4 (66.7%)	2 (33.3%)	0
16-18	13	0	9 (69.2%)	3 (23.1%)	1 (7.7%)
19-21	11	0	5 (45.5%)	6 (54.5%)	0
22	5	0	1 (20.0%)	4 (80.0%)	0

Trading Grooming for Handling?

As per the 0-3 month group, analyses of randomly selected events (N = 125) showed that the likelihood of grooming occurring with handling was low (4-6 months: 14.9%; 7-9 months: 12.1%; 10-12 months: 10.0%; 13-15 months: 16.7%; 16-18 months: 7.7%; 19-21 months: 9.1%; 22 months: 0%).

Handling Outcomes

Since older infants become able to resist or tolerate handling without intervention from their mother, a further two categories were added to reflect this progression. Therefore, for randomly selected events for which the outcome of handling attempts were known (a subset of approximately half of the 125 randomly selected events, due to differing data collection protocols between observers and the inclusion of sometimes incomplete ad libitum data from non-focal animals, N = 59) infants resisted without intervention from their mother 15.3% of the time, the same percentage of events that ended with the handler grooming the mother. The handler left in 20.3% of cases, and the

mother resisted in 28.8% of cases. The remaining 20.3% of cases resulted in the mother and infant passively tolerating the handling attempt. Thus, the outcome of handling in older infants differ from younger infants in that it is less likely to be tolerated after 4 months of age (age breakdown, Tab. 03.02).

Tab. 04.02. Outcomes of handling in infants aged 4-22 months, for randomly selected events (N = 59).

		Outcome				
Age (months)	Total N	Handler Leaves	Handler Grooms Mother	Mother Resists	Infant Resists	Mother/Infant Tolerate
4-6	28	5 (17.9%)	6 (21.4%)	7 (25.0%)	3 (10.7%)	7 (25.0%)
7-9	19	2 (10.5%)	2 (10.5%)	8 (42.1%)	5 (26.3%)	2 (10.5%)
10-12	6	3 (50.0%)	1 (16.7%)	2 (33.3%)	0	0
13-15	1	1 (100%)	0	0	0	0
16-18	3	0	0	0	1 (33.3%)	2 (66.7%)
19-21	2	1 (50.0%)	0	0	0	1 (50.0%)
22	0	0	0	0	0	0

Next, outcomes that were determined by the handler were excluded (handler leaving or handler grooming mother) and grouped the infant and mothers' responses, to compare the rate of mother/infant resistance vs. tolerance to maternal outcomes analysed for younger infants (where there was a non significant trend towards tolerance). Again, resistance appeared more likely than tolerance in almost all age groups (Tab. 04.03), but this tendency was only above chance level (50%) in the 7-9 month category (binomial (0.5) P = 0.007, 2-sided; Tab. 04.02), with insufficient data available to carry out tests for months 10+.

Tab. 04.03. Responses to handling attempt, excluding determined by the

handler, such as handler leaving or grooming the mother. Binomial tests were carried out on randomly selected dyads (N = 37; test statistic = 0.5).

		Handling Outcome		
Age (months)	Total N	Mother/Infant Resist	Mother/Infant Tolerate	Binomial P (2-tailed)
4-6	17	10	7	0.148
7-9	15	13	2	**0.003**
10-12	2	2	0	
13-15	0	0	0	
16-18	3	1	2	

Dominance Effects on Grooming and Grunting

Rank distance (range: -8 to +9) did not have a significant effect on the likelihood that grunting would occur in either the 4-6 month (N = 47 events; median rank difference: handling with grunting: 2, handling without grunting: 1; inter quartile range: handling with grunting: 5.5, handling without grunting: 8; Mann-Whitney U test Z = -1.471, P = 0.144) or 7-9 month (N = 33 events; median rank difference: handling with grunting: 4, handling without grunting: 2; inter quartile range: handling with grunting: 4.8, handling without grunting: 7; Mann-Whitney U test Z = -0.977, P = 0.338) age groups, though higher ranking handlers tended to grunt more than lower ranking handlers (months 4-6: higher = 44.4%, lower = 30.0%; months 7-9: higher = 41.7%, lower = 22.2%). For months 10+, insufficient data were available once random events had been selected.

Whether the handler was higher or lower ranking than the mother also did not have a significant effect on the likelihood that grunting would occur for either

the 4-6 month (N = 47 events, X^2 = 1.014, p = 0.374, 2-sided) or 7-9 month (N = 33 events, X2 = 1.069, p = 0.429, 2-sided) age group when random events were selected. Again, for 10+ months there were insufficient data available for analyses once random events had been selected.

The percentage of events in which grooming occurred was slightly higher but not significantly higher for higher-ranking handlers than lower-ranking handlers during months 4-6 (higher = 14.8%, lower = 15.0%; N = 47, X^2 = 0.00, p = 1.00, 2-sided) and 7-9 (higher = 4.2%, lower = 33.3%, N = 33, X^2 = 5.227, p = 0.052, 2-sided). Once random events had been selected, there were insufficient data to analyse effects of grooming associated handling in infants aged 10+ months. Thus, there were no dominance effects on grooming associated with handling in older infants.

The data for older infants show different patterns to those for younger infants. The number of cases of handling without accompanying behaviour differed depending on rank (higher ranking: N = 37, lower ranking, N = 29), while in a reversal of the pattern seen in handling of younger infants, handlers who outranked mothers groomed were equally likely to groom as those who did not (higher ranking: N = 4, lower ranking N = 4). Higher ranking handlers grunted in more cases than lower ranking handlers (higher ranking: N = 34, lower ranking: N = 15), suggesting that grunting signal benign intent, though this was not seen in handling directed at infants ages 0-3 months. Additionally, the proportion of handling that comprised attempts to forcibly remove infants was higher in every category of accompanying behaviours, for both higher and lower ranking handlers (Fig. 04.04).

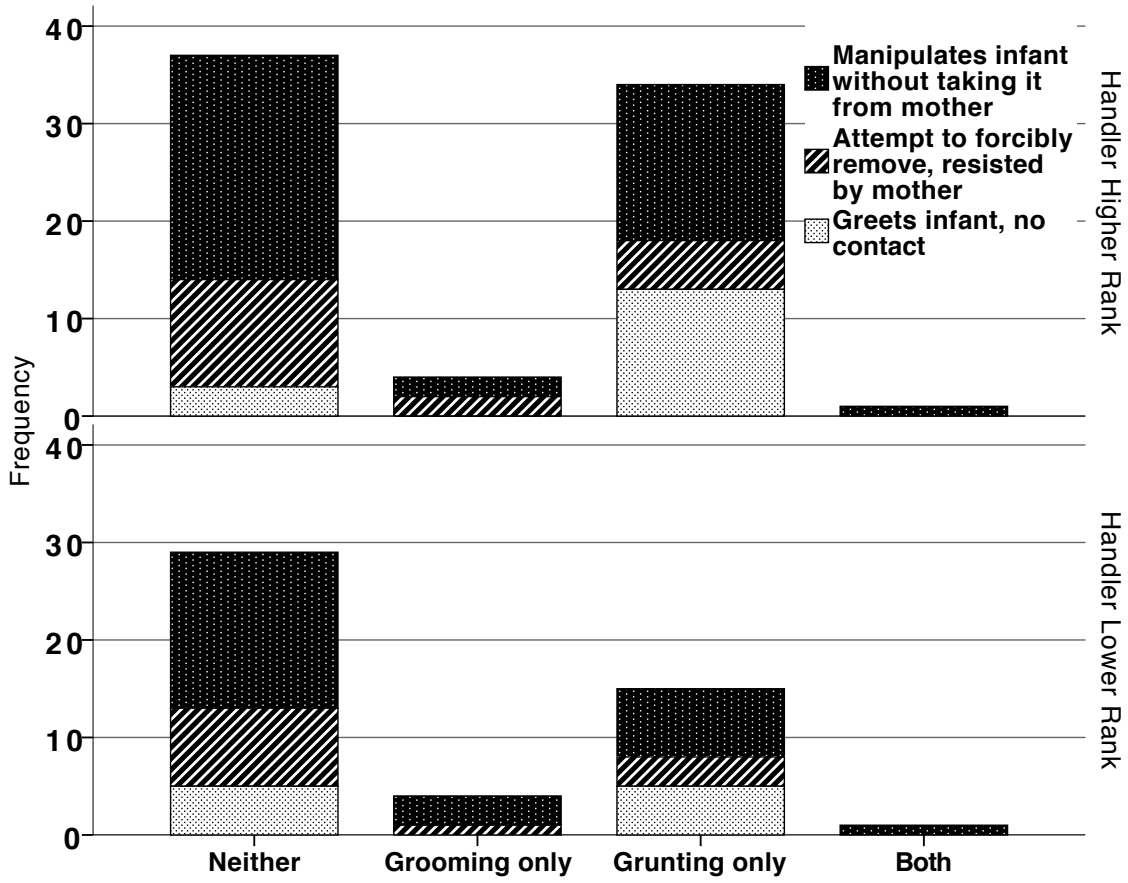

Fig. 04.04. Variation in the frequency of each handling type, in relation to the occurrence of grooming and grunting, for high (N = 76) and low ranking (N = 49) handlers. Data presented are random selected dyads for infants aged 4-22 months.

Assessing the Market Value Theory with Generalised Linear Mixed Models

Several key variables were chosen to test for dominance effects on handling in Kwano baboons, since it was predicted that power differentials should affect infant handling in a species where female status is important.

For the following set of analyses, a composite measure of handling as positive or negative was used as the dependent variable, where positive handling comprises all affiliative behaviours such as muzzle contact and embracing infants, and negative handling comprises aggressive behaviours such as grabbing, pulling and forcibly removing infants. A logistic regression with individual identity entered as a random factor was carried out to investigate whether handling type (positive/negative scored as 1 and 0) is affected by rank distance (range: -8 to +9), month of life (0-3), and presence of grooming (yes/no). This also confirmed that together, these factors did not affect handling type (X^2 = 4.62, N events = 480, df = 3, p = 0.202). While none of these factors had a significant effect on handling type individually, rank distance reached marginal significance (month of life: z = 0.96, p = 0.339; grooming: z = -1.03, p = 0.303; rank distance: est. = -0.05, SE = 0.03, z = -1.75, p = 0.080). Thus, the model suggests that there is a non-significant tendency for handlers who are higher ranking relative to the mother to handle infants more negatively.

DISCUSSION

Does Grooming Buy Access to Infants?

One main goal of this study was to explore whether biological market theory can explain infant handling in a primate in which allo-mothering is not observed and mothers therefore have no direct benefits from handing their infants over to other females.

In chacma baboons, grooming was generally rare in relation to infant handling

(22.9% of bouts; Henzi and Barrett 2002), but if it occurred it led to a high percentage of mothers tolerating handling (90.9%; Henzi and Barrett 2002). In the Kwano group, grooming associated with handling occurred at a similar rate (22.2% of events) but did not lead to increased tolerance, since it usually occurred after handling attempts. With no grooming offered before handling, mothers tolerated 77.8% of handling, suggesting that grooming was not the 'price paid' for access to infants in this study group.

What could account for the differences across different populations of baboons? It is possible that differences in grooming patterns are a direct response to the different handling behaviours, notably the rarity of olive baboon handlers forcibly trying to remove infants from their mothers. Perhaps, 'handling' is a misnomer in this species, as infants are rarely removed from their mother, though the type of interactions described here (grabbing, muzzle contact etc.) take place frequently.

In line with predictions and previous work (Frank and Silk 2009), grooming of mothers was less likely to be reciprocated in Kwano group than grooming of non-mothers, suggesting that, if grooming was traded, then this was mediated by the presence of infants. It has previously been suggested that mothers may attract grooming as a consequence of the increased stress associated with being harassed for infant access (Tiddi et al. 2010) or that it signals benign intent (Slater et al. 2007). In Kwano group, since grooming frequently occurred after a handling attempt, or both before and after, it may also function to simply maintain proximity. Since high ranking females frequently displace lower ranking peers, one would expect a low ranking mother to simply move away when approached by a high ranking handler that did not indicate benign intent,

thus preventing any attempt at handling. An approach while grunting might signal benign intent, but once the handler has approached, the mother may leave soon after even if she is not initially displaced. If a handler approaches then grooms, the mother may tolerate multiple attempts at handling during a grooming bout. Even when a handler approaches and attempts to take the infant without grooming beforehand, grooming afterwards will keep the mother present and increase the chances of multiple handling attempts.

Biological Market Theory

A biological market for infant handling seems most plausible in species where allo-mothering is frequent, as mothers gain from extra caregivers and handlers presumably gain from acquiring mothering skills (Fairbanks 1990). This is a key condition of the theory, as both parties must benefit to establish a sustainable market (Noë and Hammerstein 1994). In baboons, however, systematic allo-mothering is not observed (e.g. Altmann 1980), and there is no evidence that baboon mothers gain anything from allowing their infants to be handled - while there is evidence that infant handling can be extremely costly, resulting in injury or even the death of the infant (Kleindorfer and Wasser 2004). The peculiar absence of allo-mothering in baboons may be due to the nature of their social behaviour constrained by a strict dominance hierarchy (McKenna 1979). Indeed, across species of macaques characterised by differing social behaviour, it has already been demonstrated that the nature of handling determines the possessiveness of mothers (Maestripieri 1994c).

Biological market theory has successfully explained other types of baboon behaviour, particularly alliance formation (Noë 1990). However, in olive

baboon infant handling it has little explanatory power. The interplay between resource holding capacity, control over resources and market value (Noë et al. 1991) does not seem to be straightforward when dealing with a commodity such as an infant that is available to all adult females in a group, as females of all ranks reproduce. While grooming bout duration did seem to vary depending on how many infants were present in the group (for higher ranking handlers only), this significant difference was only between zero and two infants. The significant result for only one pairwise comparison does not equate to evidence of a market for infants, as there may be simpler explanations, for example one might expect an infant that is 'unique' in the group (in this case the only infant present with a distinctive black natal coat) to attract more attention. This does not necessarily imply that an extended grooming bout can be traded for access to that infant, particularly with the majority of grooming occurring after handling attempts. Moreover, the expected differences in behaviour associated with rank were not observed – of all the dominance related tests replicated according to Henzi and Barrett's method, only one reached significance - that of rank distance and the occurrence of grooming with handling, with lower ranking handlers more likely to groom. However, since the results of the replicated analyses can only reliably be used to make direct comparisons with the original paper due to pseudo-replication issues, it is not possible to conclude that this one significant result constitutes evidence that rank distance effects whether or not grooming occurs with infant handling in olive baboons.

Moreover, when using a GLMM, rank distance only reached marginal significance in relation to the type of handling. Thus, the evidence for dominance affecting infant handling behaviour is weak. This was true when

replicating more traditional statistical methods used by Henzi and Barrett (2002) and when analysing affects of dominance using GLMMs, allowing for use of the full dataset. There is some evidence of rank distance having an affect on infant handling behaviour, but with only one significant result that cannot be generalised, and one marginally significant result, the evidence is much weaker than hypothesised in this group. Hypotheses were based on the idea that olive baboons have a strict dominance hierarchy (Smuts 1985), though perhaps in Kwano group the situation is more complex. Although the dominance hierarchy in this group is linear, aggressive interactions are very rare, and data collected over 2 years were needed to form the linear hierarchy (Alberts 2013). Therefore, the gradient of competition may be shallow, i.e. the cost of competition to subordinates may be low (Barrett and Henzi 2003). The gradient of competition has been linked to food availability (Barton and Whiten 1993), and thus in a very productive environment such as Kwano (Warren 2003, detail of available foods chapter 2) the necessity for such competition may be low. Therefore, despite linearity on the dominance hierarchy, the power differential between two individuals several ranks apart may be small. For example, a handler with a relative rank of -5 in Kwano group may actually be equivalent to a handler with relative rank of -1 in groups with a high gradient of competition. Therefore, while not confirming expectations for an olive baboon group, the likelihood that power differentials between females are low provides a further explanation of the lack of a biological market for infants in the current study.

Is the Mother in Control of the Handling Transaction?

The fact that mothers were not more likely to tolerate handling when grooming

occurred, but tended to tolerate it passively regardless of grooming, suggests that mothers had little influence in this process. There were no indications that mothers were ever prepared to give up their infants, but rather were forced to accept handling by others. The fact that mothers reciprocate grooming less often than non-mothers could be a simple bi-product of the fact that mothers find it harder to engage in grooming interactions when nursing and carrying an infant (Frank and Silk 2009), rather than mothers using their infant as a bargaining tool to increase investment from others.

While the data do not support a market value theory of infant handling, some findings are more consistent with the alternative hypotheses: the notion that females interfere with each other's reproductive efforts or that infant handling is a bi-product of selection for maternal responsiveness.

Female Reproductive Competition

Observations strongly suggested that infant handling was costly to both the mother and the infant in terms of harassment and prevention of nursing, with no indications of benefits for them. As the data support the theory that handling is not beneficial to olive baboon mothers, it is possible that it may harm their future reproductive success, and indirectly benefit handlers. When handlers managed to take an infant from its mother, the manipulation remained brief, with handlers dropping or releasing the infant soon after obtaining it. Therefore, the handling interaction seems to be driven by a desire to remove an infant from its mother, rather than subsequent possession of it. Moreover, being a mother of an infant under three months of age did not affect handling rates, further supporting the theory that possessing an infant is not the goal of

handling in olive baboons; mothers of young infants still attempt to handle other infants of a similar age. However, the handler's goal does not seem to be overtly aggressive: when the opportunity arises, and the infant is separated from its mother, handlers do not attack or kill it, and therefore handler benefits are only indirect. It is likely that straightforward aggression and forced handling would not be beneficial even when higher ranking individuals could achieve this, as the mothers would not tolerate future proximity to such handlers. Indeed mothers tend to react as though the mere approach of some individuals is a threat (Altmann 1980). Annecdotal scenario (c), in which a handler removed a mother's nipple from the mouth of her infant, further supports the idea that benefits are derived indirectly by preventing infants from nursing.

In the current study, females of all ranks attempted to handle infants regardless of relative rank. For example, females ranking 5 places below the mother were equally likely to attempt handling her infant as females ranking 5 places above the mother. This is consistent with behaviour expected if handling is beneficial to the handler at the cost of the mother. Aggression against handlers was rare, therefore it is a low risk behaviour that could prove beneficial. Additionally, rank does not give an advantage in the success of handling, therefore lower ranking mothers are equally able to resist. This has also been observed in yellow baboons (Bentley-Condit et al. 2001) and supports the idea that the predominant response to handling is one of not giving up an infant.

The occurrence of grooming after infant handling is consistent with a previous study on olive baboons (Frank and Silk 2009) but does not seem to be consistent with female reproductive competition. If handlers are only interested

in harassing the mother and infant, and their benefits are derived from preventing it from nursing and causing stress, there is no reason for them to groom after handling instead of simply leaving. It is important to note that the vast majority of handling did not involve any grooming, and it was as likely for handlers to leave, and far more common for them to rest next to the mother without grooming, than to groom – outcomes that are consistent with this hypothesis. Additionally, the genetic relationships between adult females in Kwano group are not yet known, so there may be an undocumented effect of kinship on handler behaviour, as observed elsewhere (Schwartz et al. 2003). Nevertheless, our data support some but not all elements of the female reproductive competition hypothesis.

Bi-product of Maternal Motivation

Unlike the female competition hypothesis, bi-product theory can account for the lack of overt harm inflicted upon infants – if attempts to handle infants are a result of selection for maternal responsiveness, while behaviour such as grabbing may seem aggressive, it would not necessarily be intended to harm the infant, or indeed have that result. For example, infants of Indian langur monkeys are routinely handled roughly, but do not seem to be harmed in the process (Sommer 1989).

In the annecdotal data scenario (a) the female's adoption of an unrelated infant could be the result of selection for maternal care, despite the high costs. Similarly, in qualitative scenario (b) the continued attraction to a dead infant could be explained by bi-product theory, as the visual cue of a black infant without movement or sound was sufficient to attract handlers, suggesting that

some individuals are indeed highly responsive to the presence of infants.

Older Infants

Handling of older infants is generally distinguished by an increase in more aggressive attempts to take an infant, and a decrease in the overall number of attempts. It is also more likely that mothers and infants will resist handling attempts rather than tolerate them at ages 4 months and above, a reversal of the tendency to tolerate handling when infants are aged 0-3 months, though this tendency was not significant. This supports the theory that infant handling is a form of harassment; mothers seem more likely to resist when the number of attempts at handling decrease, making resistance a practical solution.

In older infants, it was not practical to test all the hypotheses of the market value theory. Having found no evidence of a market for infants aged 0-3 months, it was not expected that such a market would emerge at later ages. As per younger infants, grooming associated with handling was rare and more likely to occur after handling. At this age, grooming seems unlikely to serve the purpose of maintaining proximity to the infant when older infants spend the majority of their time away from their mothers. Therefore, maintaining proximity to a mother in the absence of the infant would not lead to greater access – potential handlers would be more successful pursuing infants independently in order to make contact with them, and this would not be classified as infant handling as defined here.

It is possible that the behaviour observed in older infants is an entirely different interaction. For infants aged 0-3 months theories have, perhaps necessarily, focussed on the handler-mother interaction and treated the infant as passive.

At very young ages, the infant and mother do indeed come as a pair in which the infant could be traded if the mother wished, but become much more independent as they age. Approaching infant handling from an infant socialisation perspective, using observations spanning a greater age range, enables one to observe infants becoming involved in attempts to remove them from their mothers. In addition to resisting handling attempts physically (e.g. pulling away from a handler) infants can be very vocal in response to handling attempts (see chapter 6). This may further encourage mothers to resist handling attempts since infant vocalisations can aggravate bystanders, potentially endangering the infant and mother.

Defining the Infant

Of course as infants age, less time is spent in contact with their mother (chapter 3). Since handling continues, it is possible that clinging or nursing (behaviours that are common in young infants) act as a cue for potential handlers – while alone, a 22 month old infant is indistinguishable from a juvenile, and defined as an infant for our purposes only because it continues to nurse occasionally.

The greater percentage of data included in the 4-22 month age group reflects the repetitive nature of handling of younger infants – while the overall number of handling attempts is larger for months 0-3 than the entire remainder of the dataset spanning 4-22 months, much of it is excluded when selecting one event per handler/infant. For older infants, the percentage of time spent in contact with the mother is low, and infant handling requires infants to be in contact with their mother by definition, so that handlers can attempt to remove

that infant. Therefore, the time available for handlers to attempt to handle infants is very restricted, and the fact that it still occurs suggests that the act of removing infants from their mothers is a strong motivation for adult females.

Conclusions

Overall, the data do not provide evidence of a biological market effect in infant handling, but can be interpreted using both the female reproductive competition hypothesis and the maternal bi-product theory. These explanations are not mutually exclusive: a motivation to handle infants may come from selection for maternal responsiveness, with the indirect harm done to infants, benefitting handlers' future reproductive success. However, no single theory seems to be able to account for all of the handling behaviour observed in olive baboons. Moreover, both theories focus exclusively on adult females as handlers, and thus by definition cannot explain the 27.7% of handling carried out by adult males and juveniles. Thus, the issue of why baboons attempt to handle unrelated infants remains largely unresolved. Certainly, biological market theory does not provide a comprehensive answer.

SECTION III:

INFANT COMMUNICATION

CHAPTER 5:

THE VOCAL REPERTOIRE

Infant Emma with his mother Ymke at 2 months of age, with sub-adult Murna and an adult male nearby. Photo: Suzanne Harvey, 2010.

INTRODUCTION

Thus far, infant socialisation has been approached from a behavioural point of view, with adult vocalisations associated with infant handling forming the communication element of infant centred interactions. The literature tends to approach infant centred interactions from this exclusively adult perspective, as exemplified by the Market Value Theory of infant handling, in which the infant is a passive commodity that adults can trade (chapter 4). Studies of baboon communication also overwhelmingly focus on adult vocalisations, with only two mentions of infant olive baboons vocalisations (Byrne 1981; Wallez and Vauclair 2012) with the latter focusing on such calls. Before attempting to investigate the information contained in infant vocalisations, it is first necessary to define the infant vocal repertoire.

In addition to the fact that infant vocalisations have been largely neglected in this species, studies into adult vocalisations have shown interesting acoustic variation. Acoustic analyses and playback experiments have shown that the most common adult vocalisation, the grunt, is in fact two different call types (Rendall et al. 1998). Unlike general affiliative grunts, 'infant' grunts only occur in specific instances of an adult approaching an infant and attempting to handle it, and thus this category describes two different types of vocal behaviour that should be distinguished. Therefore they are often referred to as dichotomous 'infant/affiliative' and 'move' grunts. Playback experiments have shown that individuals distinguish between these two types, and produce functionally distinct responses (infant grunt variants: Cheney et al. 1995a; affiliative grunts: Cheney at al. 1995b; both: Owren et al. 2002). In chacma baboons, acoustic analyses have also been used to distinguish between

contact barks and alarm barks (Fischer et al. 2001). Moreover, infant responses to these different bark variants only become accurate at around six months of age (Fischer at al. 2000), suggesting that some calls need to be learnt by infant baboons, and are not understood from birth.

Since adult baboon vocalisations are acoustically variable but can be reliably grouped into specific call types, it is to be expected that infants are also able to produce specific vocalisations. This would suggest that infant vocalisations communicate information to listeners and are not simply meaningless sounds. The alternative, that sounds are produced with high variation in acoustic features and cannot be grouped into separate types of vocalisation, would imply that the ability to use specific sounds to communicate information is developed some time during infancy, in order to function as a member of the adult social group. Therefore, acoustic features are analysed here as an initial confirmation of classification of different call types.

Production of Vocalisations

The various components of speech production are commonly understood using the source/filter theory (Hixson 1973, Fitch 2000, reviewed in Taylor and Reby 2010), and this process is very similar in humans and non-human primates. Firstly, air is expelled from the lungs, causing oscillation of the vocal chords in the larynx. This rate of oscillation determines the pitch of a sound that is produced, measured in hertz. Acoustic energy then passes through the vocal tract, where the sound is filtered. It is this filtering process that produces formants, by restricting some frequencies and allowing others to pass through unfiltered. Importantly for studies into the ontogeny of vocalisations, the size

and shape of the vocal tract (including oral and nasal cavities as well as the trachea) result in the production of higher pitched sounds by individuals with shorter vocal tracts, such as infants (Fitch 2000).

In addition to such ‘voiced’ sounds, sound can also be produced by the glottis, a term used to refer to the vocal chords together with the air spaces between them (Hixson 1973). The glottis is used to produce voiced or unvoiced calls; a glottal stop is produced by restricting the air in the glottis rather than vibrating the vocal chords. In English, the sound denoted by the letter ‘h’ is an example of this.

The main difference between human and non-human vocal tract anatomy is the vertical orientation of the human vocal tract that evolved alongside bipedalism (Negus 1949). In addition to the environmental and social conditions modern olive baboons share with early hominids, the anatomy of their vocal tracts is also peculiarly similar to humans, since the descent of the larynx is a secondary sexual characteristic in humans, and thus occurs during puberty (Patra et al. 1986, Mardini et al. 1987, Blitzer and Meyer 2006; Fig. 05.01) making this species an excellent model for studying call production and the acoustic features of vocalisations. It has even been noted that infant human vocal tracts share more similarity with those of non-human primates than adult humans (Lieberman et al. 1971).

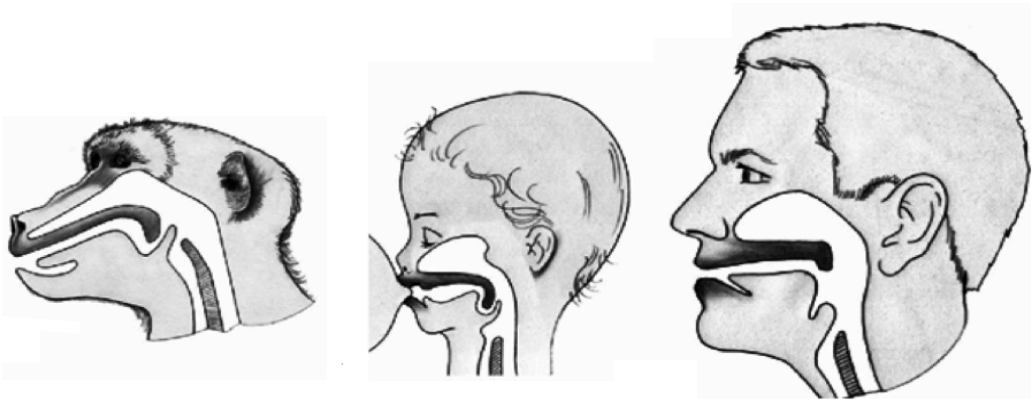

Fig. 05.01. Vocal tract anatomy of a baboon, human infant and adult human (L-R). Adapted from Blitzer and Meyer 2006.

One theory of acoustic variation in mammalian calls is based on motivation-structural (MS) rules, which state that aggressive vocalisations should be low pitched and noisy, while fear-related vocalisations should be high pitched and tonal (Morton 1977). A key assumption of the MS rules is that body weight is inversely correlated with the pitch of vocalisations via vocal tract length, linked to larger animals frequently being dominant over their smaller peers. However, this theory does not include infant vocalisations, whose vocal tracts are shorter regardless of dominance, and vary according to age rather than dominance hierarchy. Therefore, it is predicted that all infant vocalisations will be higher in pitch than adult vocalisations, but variation between call types may reflect the emotional states associated with each call. Aggressive interactions are very rare in infants, so it is unlikely that low pitched noisy calls will be recorded, but fear reactions are common, and thus it may be predicted that calls will be on a spectrum of high pitched, noisy or tonal sounds depending on their context.

Furthermore, a test of this hypothesis in 36 non-human primate species (Hauser 1993) supported the hypothesis regarding pitch variation, but not tonality. Thus it is likely that pitch but not tonality will vary in infant baboon calls.

Acoustic measures

There are of course a great number of acoustic variables available for analyses, and those likely to reveal the most about the information communicated by vocalisations must be selected. Infant barbary macaque vocalisations have been shown to vary in 84 different parameters, though the start frequency, high frequency parts, mean median frequency and duration are sufficient to classify calls (Hammerschmidt and Todt 1995). For the current study, duration, peak frequency, and the change in frequency in the first and second halves of the call, referred to as 1st and 2nd half frequency modulation have been selected to describe each call.

MATERIALS AND METHODS

Data Collection

Audio recordings were made using a Marantz P660 Solid State Recorder with a Sennheiser ME66 directional microphone. Recordings were made from 1-10 m away, though it was usually necessary to record grunts and moos from a distance of 3 m or less to obtain sufficient quality, as they are quieter than other vocalisations. Recordings were discontinued when background noise was too loud, e.g. in river beds and during movement through fallen leaves.

Following equipment damage, additional audio files were recorded using a Panasonic SDR-H100 camcorder, and extracted from video files using iMovie version 8.0.6. All files from both recording devices were produced as uncompressed AIFF files, a 'lossless' format developed for Mac OS X that allows data to be perfectly reconstructed from the compressed file (Apple Computer Inc 1989). After selecting calls for quality, 8 of 103 were sourced from the camcorder. These recordings produced clear spectrograms for analyses, and though small in number were deemed comparable to recordings made by the Solid State Recorder, as they were not outliers in any of the parameters studied (see acoustic parameters, below).

As adult vocalisations were not the focus of data collection and focal follows were only carried out for infants only, samples of adult vocalisations were taken from ad libitum recordings of interactions within 5 m of the infant focal animals.

Analyses

In order to measure the acoustic features of a call, spectrograms must first be produced. A spectrogram is a visual representation of the sine waves that constitute a complete waveform, or sound. The sine waves on a spectrogram show the energy levels in a call over time. Visually, the darker the waves appear, the more energy is present at that frequency.

To document the acoustic features of the infant olive baboon vocal repertoire, initially, all vocalisations were categorised by ear. Four distinct call types were recognisable – 'gecks, 'moos', 'screams', and the distinctive baboon 'wa-hoo' call that is commonly produced by adults. For all acoustic analyses, a Fast

Fourier Transform with Gaussian window was applied using PRAAT version 5.1.23 software (Boersma and Weenink 2010). The following spectrogram settings were used for all calls in the acoustic analyses (moos, gecks and wa-hoos): frequency range = 0-6000Hz, window length = 0.065 s, dynamic range = 30 dB. The frequency range was increased for infant screams and adult submissive pants (to 0-10000 Hz and 0-7000 Hz respectively) in order to visualise the whole call. For calls that have a very low frequency, such as grunts, additional spectrograms with a frequency range of 0-1500 Hz are provided to show the acoustic features that are not visible at 0-6000 Hz. All other settings were constant across all call types.

Acoustic Parameters

As background noise was often high even in good conditions, automated analyses of acoustic variables were found to be unreliable. Specifically, the 'pitch' function in PRAAT was unable to extract the fundamental frequency of calls. Therefore, in order to obtain a good description of each call, peak frequency measurements were taken at the beginning, middle and end of each call.

In order to calculate peak frequency, first, a 1.5 second extract including the target call, was extracted from each recording. Then, the cursor was placed at the middle of the call, in an area of dark black. Next, the 'view spectral slice' option was selected to produce a magnitude vs. frequency plot (Fig. 05.02). By placing the cursor at the highest peak of this plot, it is possible to read the peak frequency, in this case, for a wa-hoo call, 1045 Hz. This process was repeated at the beginning and end of each call. Thus, it was possible to

calculate the change in frequency in the first and second halves of the call, referred to as 1st and 2nd half frequency modulation. Using this method, the chosen acoustic parameters were calculated as follows:

- Duration: time at end of call minus time at the beginning of the call
- Peak frequency: peak frequency mid call
- Frequency modulation first half of call: peak frequency mid call minus peak frequency at the beginning of the call
- Frequency modulation second half of call: peak frequency at the end of the call minus peak frequency mid call

Taken together, these acoustic measures describe the duration, frequency and frequency contour of each call (cf. Fig. 05.02). These values were then input into SPSS version 20 for further analysis.

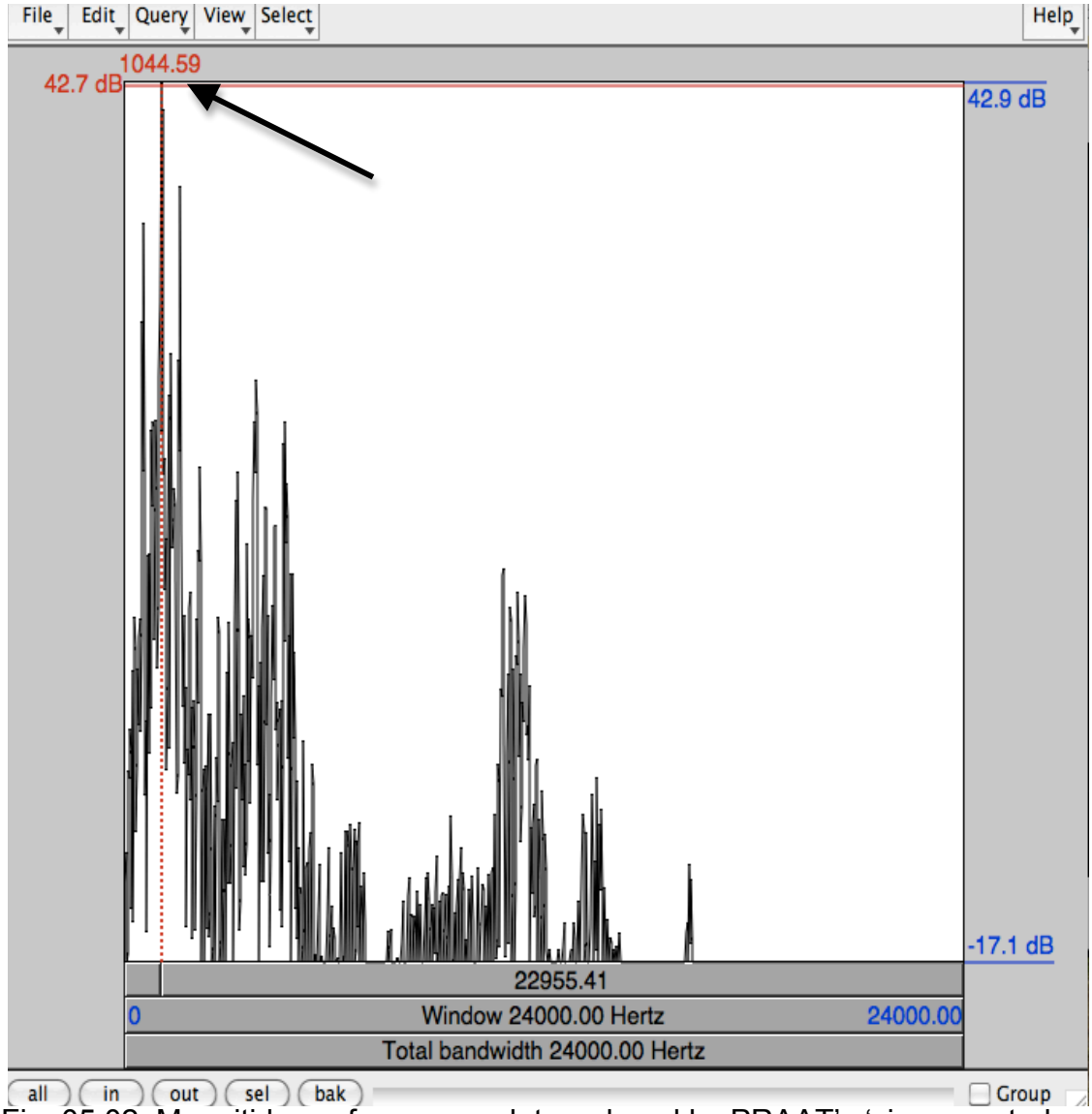

Fig. 05.02. Magnitide vs. frequency plot produced by PRAAT's 'view spectral slice' function, showing the peak frequency of a call, in this case a wa-hoo.

Since calls were recorded ad libitum, it was not always possible to determine the position of a call within a call bout. For instance, if an infant began vocalising, recordings were begun as quickly as possible, but calls produced early in a sequence may be missed. Therefore, individual calls were randomly selected from each sequence to control for the effects of bout duration (e.g. infants becoming tired, or more/less distressed as the call sequence

progresses). Throughout all acoustic analyses, a minimum of three calls per individual and per call type, from different call bouts, was an entry requirement. However, in some cases this was not possible due to the age specificity of some calls. Therefore, the number and identity of individuals, as well as the call types included in analyses are specified for each test.

Variance inflation factors were generated to measure how much any potential variance of regression coefficients would be increased due to collinearity. The resulting colinearity statistics carried out on the four parameters showed that all had acceptable variance inflation factors (VIF: < 3.0; range: 1.1 - 2.3), indicating that the chosen parameters did not suffer from colinearity. Therefore, discriminant function analyses were carried out to determine whether the call type, sex, or identity of the individual who produced the call could be reliably predicted by the 4 acoustic variables chosen.

Discriminant Function Analyses with Non Independent Data

Since it has been argued that samples including several calls from the same individuals inflate the significance of discriminability (Mundry and Sommer 2007, Waller et al. 2013. Jansen et al. 2012) analyses were repeated using permuted discriminant function analyses (pDFA; Mundry and Sommer 2007). Using the script provided by Roger Mundry (pers. Comm.), pDFAs were carried out using R version 3.0.2, GUI 1.62 Snow Leopard build.

RESULTS

Call bouts including mooing and gecking were common throughout infancy, while screams were more common in months 1-3 and wa-hoo calls were only produced later in infancy (first observed at 7 months; Tab. 05.01). Thus, different individuals are included in analyses for different vocalisations, due to their age at the time of sampling.

Tab. 05.01. Percentage of call production for all individuals, by age (N = 3597; individuals did not contribute to all call types, breakdowns given for acoustic analyses). These data do not represent frequencies as data collection included ad libitum as well as all occurrence sampling.

	Call Type			
Age (months)	Scream	Geck	Moo	Wa-hoo
1 to 3	29.1	38.3	32.7	0.0
4 to 6	10.0	47.9	42.2	0.0
7 to 9	14.5	41.1	44.0	0.3
16 to 18	13.8	40.5	37.1	8.5
19 to 21	15.2	32.2	35.7	17.0

Classifying Vocalisations

A total of 103 calls of three types were included in acoustic analyses, and call sequences were selected according to quality before an individual call from each sequence was randomly selected for analysis. Screams were excluded from analyses due to high levels of noise and difficulty in distinguishing acoustic features, and an example spectrogram is presented (Fig. 05.09) Overall, a cross-validated discriminant function analysis assigned 87.4% of cases to the correct call type (Wilks' Lambda = 0.98, X2 (df = 8) = 228.84, p =

<0.001; Fig. 05.03). Therefore, the function derived from all 4 acoustic variables accounts for a significant amount of the variance across different call types.

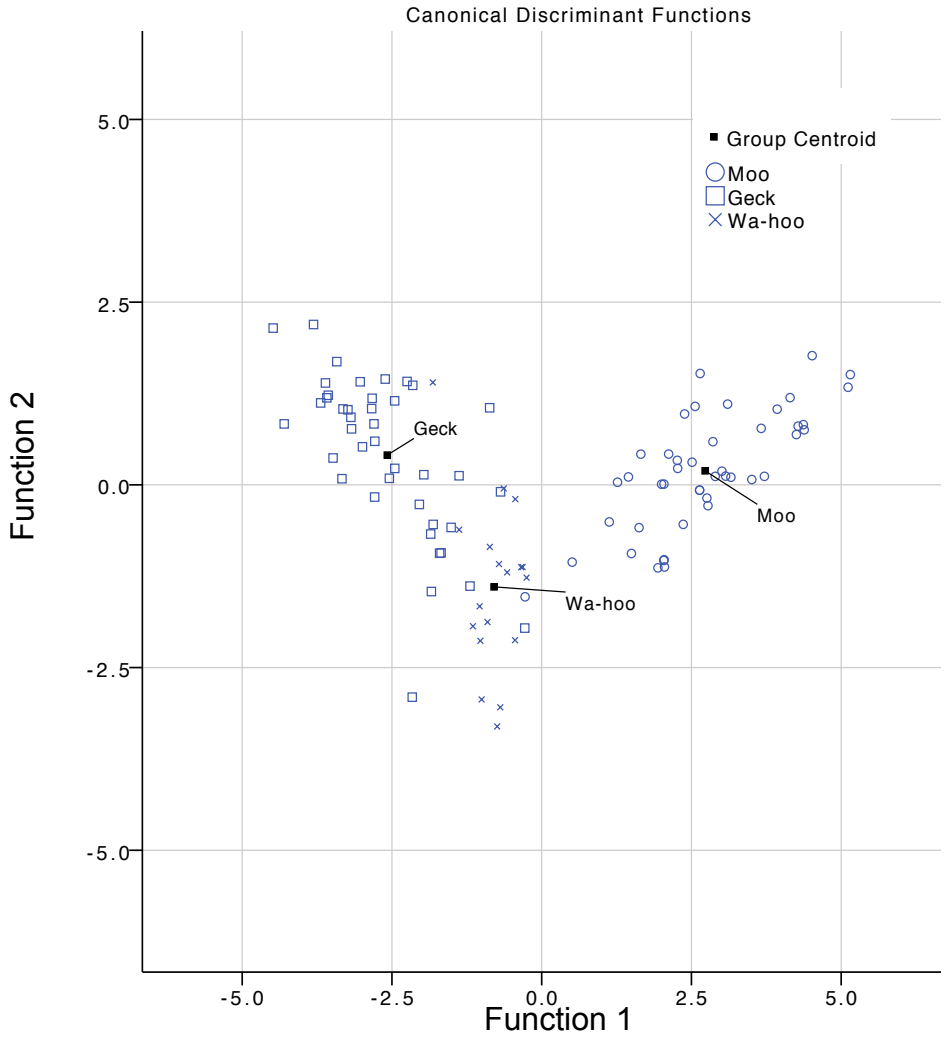

Fig. 05.03. Visualisation of the three main call types produced by all 7 infants, showing little overlap and a high percentage of correct classifications. Function 1 = duration*0.778 + 2nd half frequency modulation*0.124 – 1st half frequency modulation*0.094 – peak frequency*0.597. Function 2 = peak frequency*0.654 + 1st half frequency modulation*0.638 + duration*0.460 – 2nd half frequency modulation*0.459.

Sex and Identity

For these analyses, wahoo calls were excluded so that all individuals contributed to both call types, and thus analyses were not confounded by call type. A cross-validated discriminant function analysis revealed that the function derived from all four acoustic variables did not account for a significant amount of variation between male and female infants (Wilks' Lambda = 0.85, X2 (df = 4) = 5.77, p = 0.217). 57.8% of calls were correctly classified as male or female, which was not significantly different from chance (binomial (0.5) p = 0.188). However, a bias in the sex of infants born during the three field seasons for which data were collected (as a result of all births between December 2009 and March 2011 being male) meant that more male (N = 66) than female (N = 17) vocalisations were included in the analysis. Since only two females were represented in the sample, conclusions about sex differences must be treated with caution. Therefore, a further cross-validated discriminant function analysis was carried out comparing gecks and moos, produced by all individuals, which showed that acoustic variables again accounted for a significant amount of variation between individuals (Wilks' Lambda = 0.41, X2 (df = 24) = 68.23, p = < 0.001). Only 26.5% of cases were allocated to the correct individual, though this was still significantly above chance level for a sample with 7 individuals (binomial (0.14) p = 0.004). Therefore where possible, individual differences are investigated within each individual call type.

Wa-hoo

Wa-hoo (N calls = 18, N individuals = 3) calls are generally high pitched and of

short duration (M±SD: peak frequency = 1160.44 ± 255.94Hz, 1st half frequency modulation = -215.01 ± 268.32Hz, 2nd half frequency modulation = 106.53 ± 312.96Hz, duration = 0.16 ± 0.04s). These calls are a two syllable sound, with the pitch rising throughout the 'wa' section and lowering throughout the 'hoo' section, creating an arched pitch contour (Fig. 05.04).

A cross-validated discriminant function analysis allocating vocalisations to one of the three individuals who produced wa-hoo calls showed that the function derived from all four acoustic variables did not account for a significant amount of variance between individuals (Wilks' Lambda = 0.45, X2 (df = 8) = 10.89, p = 0.208; Fig. 05.05). Only 50.0% of cases were classified correctly, which was not significantly higher than chance (binomial (0.33) p = 0.33). Therefore, although the sample comprised two females and one male, all produced acoustically similar wa-hoo calls. Since only one male was included in the sample, it was not deemed appropriate to carry out classification statistics on sex differences in wa-hoo calls.

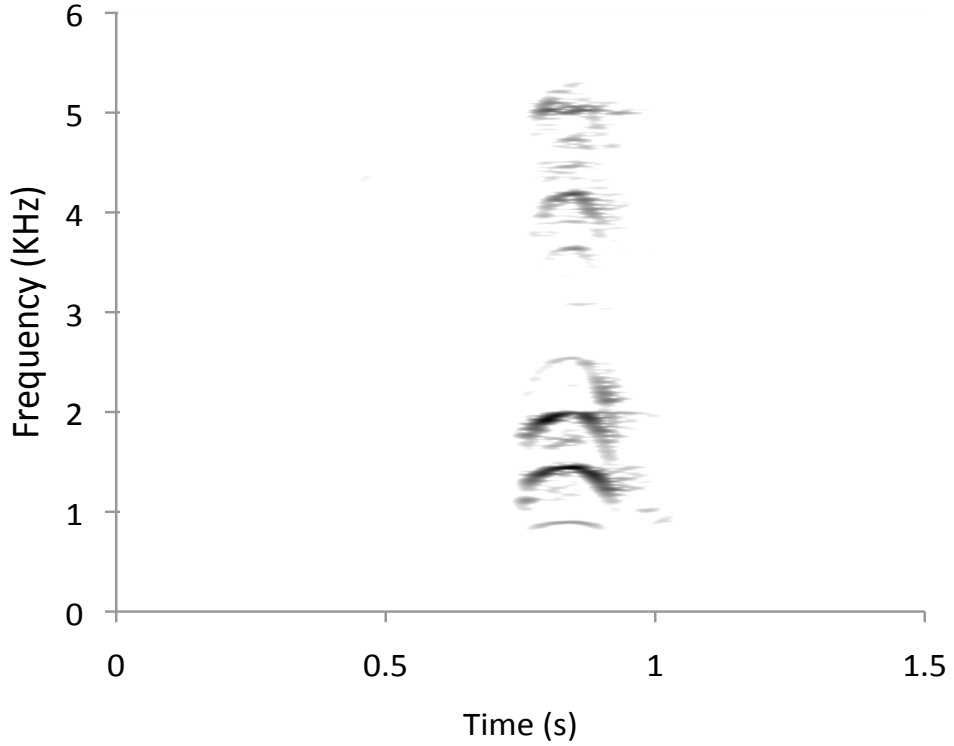

Fig. 05.04. Representative spectrogram of an infant wa-hoo call, showing an arched pitch contour with high frequency and short duration.

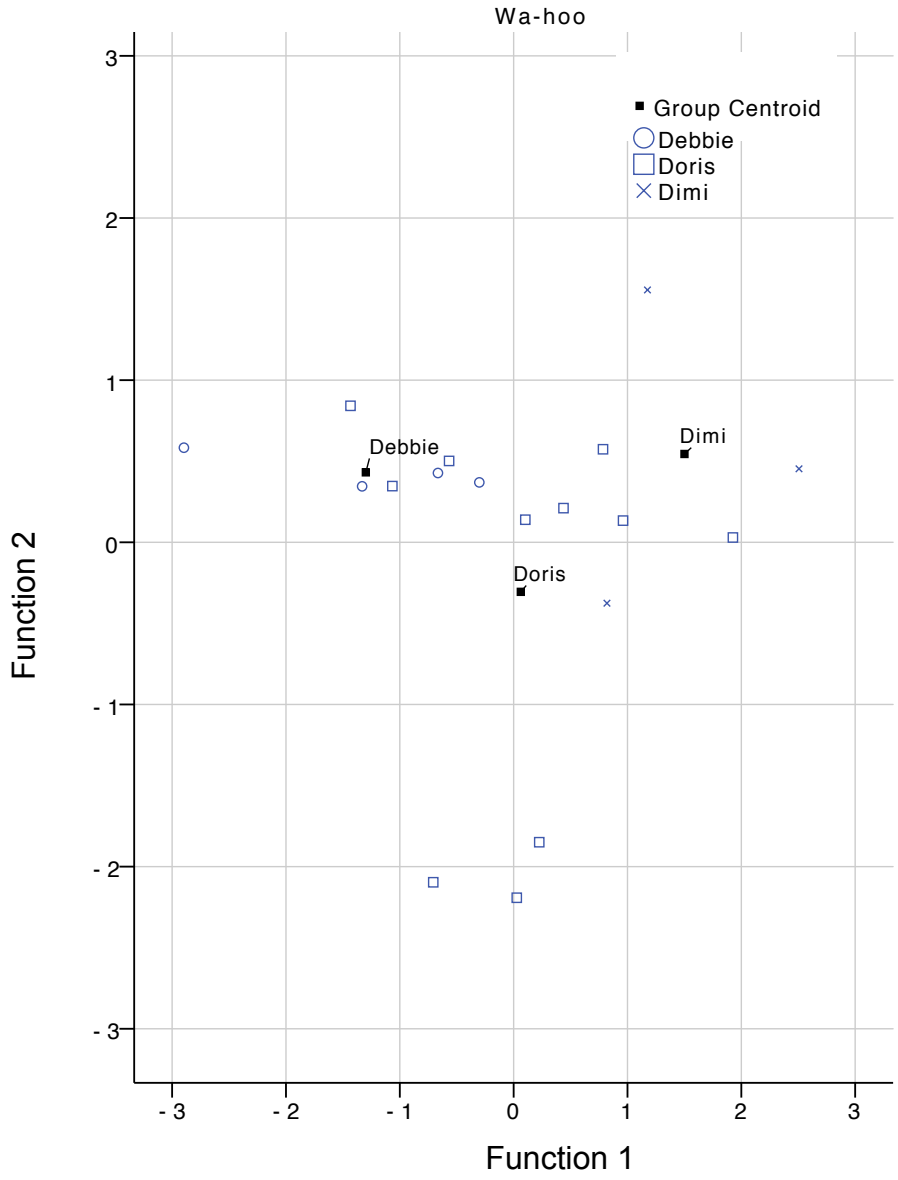

Fig. 05.05. Visualisation of a discriminant function analysis based on wa-hoo calls produced by three individuals, showing a high degree of overlap and low percentage of correct classifications. Function 1 = duration*0.880 + 2nd half frequency modulation*0.346 – peak frequency*0.215 – 1st half frequency modulation*0.314. Function 2 = peak frequency*1.017 + 1st half frequency modulation*0.136 + 2nd half frequency modulation*0.027 – duration*0.100.

Moo

Moos (N calls = 42, N individuals = 4) are a relatively long, low pitched sound produced only by infants (M±SD: peak frequency = 495.31 ± 152.23Hz, 1st half frequency modulation = -29.61 ± 124.07Hz, 2nd half frequency modulation = -12.16 ± 58.07Hz, duration = 0.62 ± 0.19s; Fig. 05.06). While the pitch is generally consistent throughout the call, in some cases it either increases or decreases towards the end of the call.

A cross-validated discriminant function analysis allocating vocalisations to one of the four individuals who produced moo calls revealed that the function derived from all four acoustic variables accounted for a significant amount of variation between individuals (Wilks' Lambda = 0.56, X2 (df = 12) = 21.07, p = 0.049; Fig. 05.07). However, only 13.6% of cases were classified correctly (Fig. 05.05), which was not significantly greater than chance (binomial (0.25) p = 0.151. An additional cross-validated discriminant function analysis with sex as the grouping variable was also non significant (Wilks' Lambda = 0.89, X2 (df = 4) = 4.19, p = 0.381) which classified 59.5% of vocalisations correctly, which was not significantly greater than chance (binomial (0.5) p = 0.28). However, this result must be treated with caution as the sample included far more male (N = 37) than female (N = 5) moo vocalisations, due to the two female infants being the oldest of the focal animals during data collection and thus producing moos less frequently.

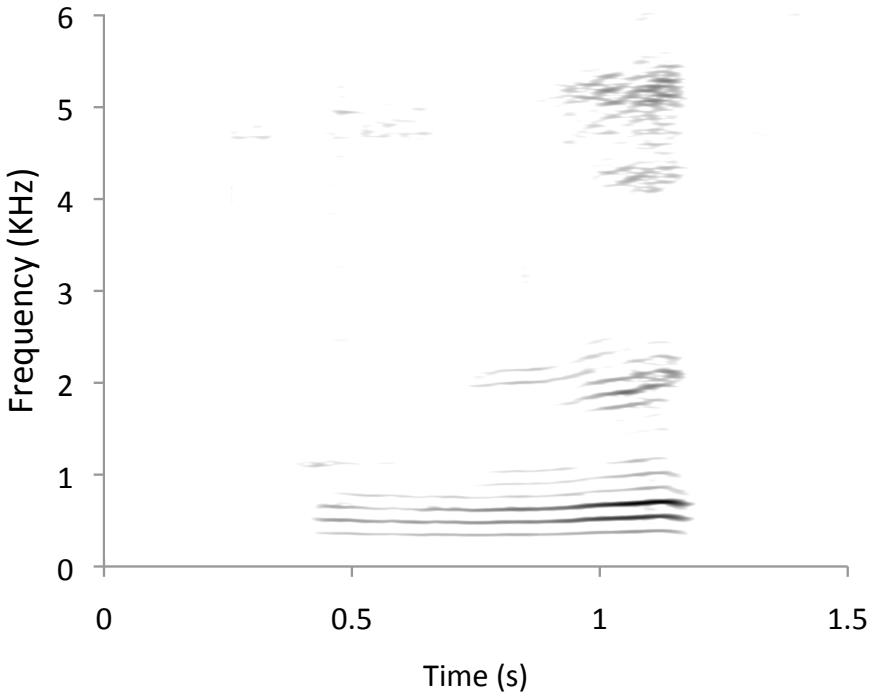

Fig. 05.06. Representative spectrogram of an infant moo call, showing a relatively flat pitch contour with low frequency and long duration.

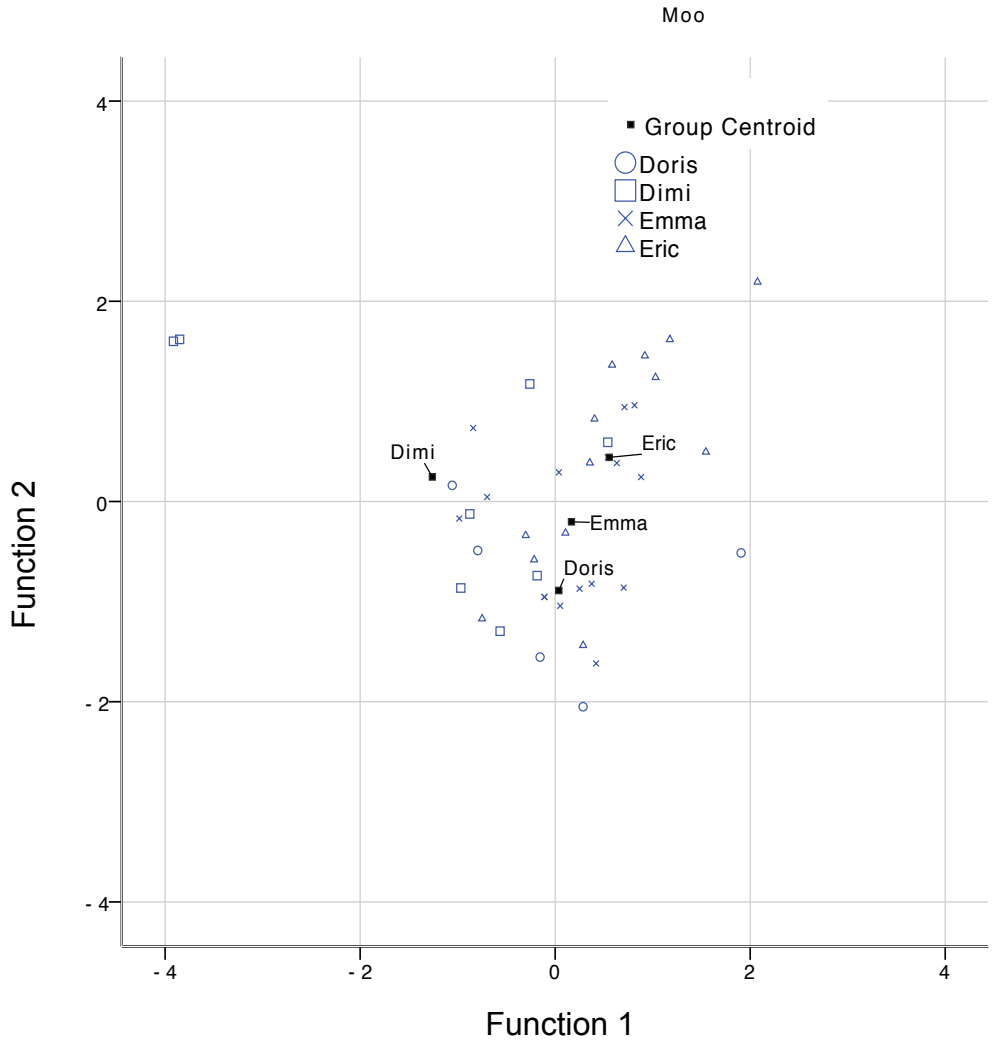

Fig. 05.07. Visualisation of a discriminant function analysis based on moo calls produced by six individuals, showing a high degree of overlap and low percentage of correct classifications. Function 1 = 2nd half frequency modulation*0.757 + 1st half frequency modulation*0.710 + peak frequency*0.376 + duration*0.338. Function 2 = peak frequency*0.737 +1st half frequency modulation*0.043 – duration*0.069 – 2nd half frequency modulation*0.383.

Geck

Gecks (N calls = 41, N individuals = 7) are only produced by infants. The call sounds like a glottal stop – i.e. a sound that is produced by obstructing airflow in the vocal tract, rather than one produced by the larynx (Fitch 2000). The geck is a very short, high pitched sound (M±SD: peak frequency = 1896.53 ± 637.71Hz, 1st half frequency modulation = -14.83 ± 169.76Hz, 2nd half frequency modulation = -13.04 ± 216.16Hz, duration = 0.07 ± 0.06s; Fig. 05.08).

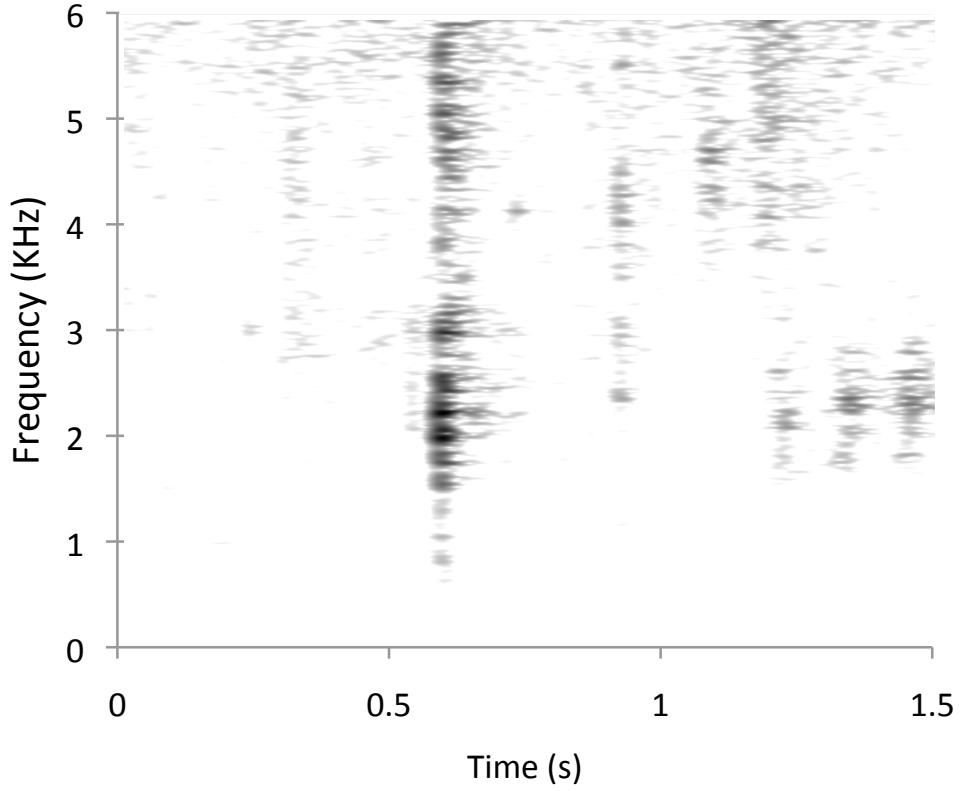

Fig. 05.08. Representative spectrogram of an infant geck call, with high frequency and short duration.

A cross-validated discriminant function analysis allocating vocalisations to one of the seven individuals who produced geck calls revealed that this is the only call type in which the function derived from all four acoustic variables is able to account for a significant amount of variation between individuals (Wilks' Lambda = 0.324, X2 (df = 24) = 38.84, p = 0.028). However, only 22.0% of cases were classified correctly, which was not significantly above chance level for a sample with 7 individuals (binomial (0.14) p = 0.177; Fig. 05.09). An additional discriminant function analysis with sex as the grouping variable was not significant (Wilks' Lambda = 0.860, X2 (df = 4) = 5.565, p = 0.234) and classified 68.3% of vocalisations correctly, which was not significantly greater than chance (binomial (0.5) p = 0.276). Gecks were the only vocalisations produced by all infants for which data were available.

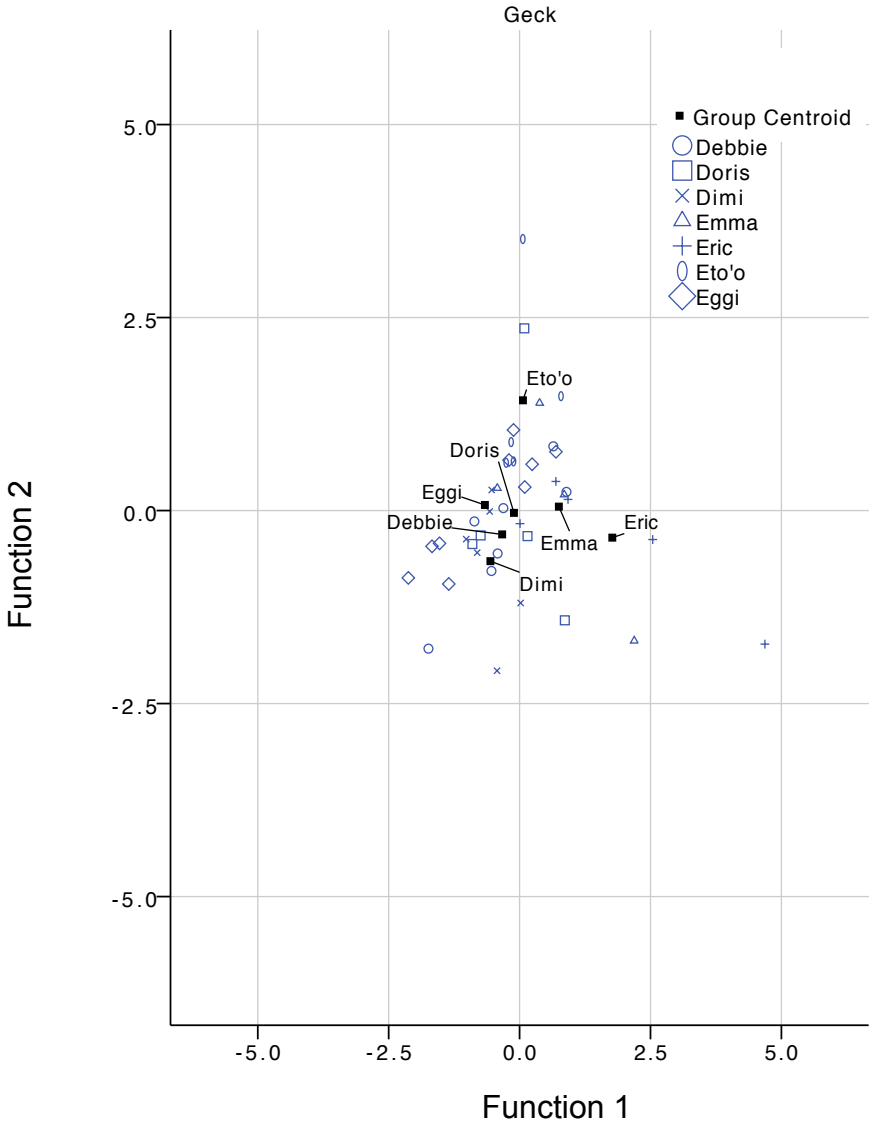

Fig. 05.09. Visualisation of a discriminant function analysis based on geck calls produced by seven individuals, showing a high degree of overlap and low percentage of correct classifications. Function 1 = duration*0.968 + peak frequency*0.686 – 1st half frequency modulation*0.003 – 2nd half frequency modulation*0.234. Function 2 = peak frequency*0.626 + 2nd half frequency modulation*0.526 + 1st half frequency modulation*0.439 – duration*0.321.

Scream

Screams were produced by individuals of all age classes, are high pitched and of varying duration (Fig. 05.10). In fact, screams were the most variable of all the infant vocalisations. This example, produced by infant male Eric, is unusual in that some acoustic features are distinguishable. Screams were not included in discriminant function analyses due to high levels of noise and atonality, which obscure the harmonics of the call.

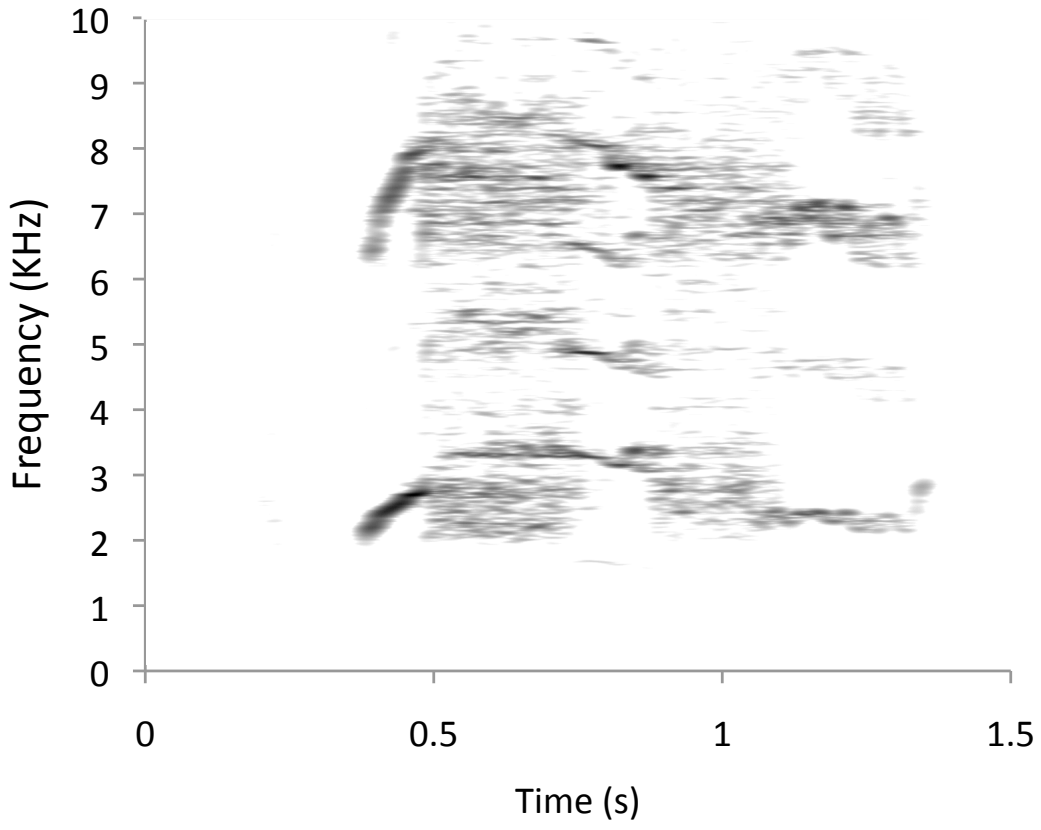

Fig. 05.10. Representative spectrogram of an infant scream, with high frequency and long duration. This call shows both tonal and atonal sections.

Adult Vocalisations

Wa-hoos and Barks

The adult female version of the wa-hoo call, also referred to as a bark, shows a similar pitch contour to the infant version (Fig. 05.11). The example, produced by adult female Ladi, was recorded as follows: peak frequency = 1239.30Hz, 1st half frequency modulation = 679.00Hz, 2nd half frequency modulation = 79.89Hz, duration = 0.19s).

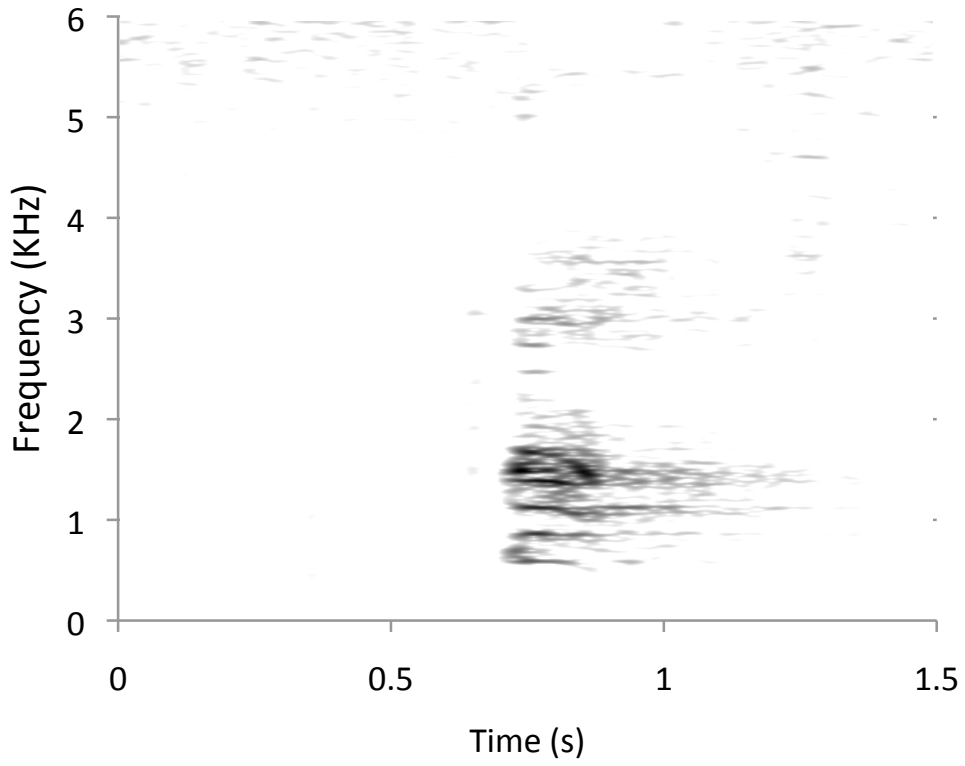

Fig. 05.11. Representative spectrogram of an adult female wa-hoo call, with a slightly arched pitch contour. The acoustic features of this call resemble those of the infant wa-hoo call.

Grunts

Adult grunts (Fig. 05.12 & Fig. 05.13) are a low frequency sound with a flat pitch contour. The example, produced by adult female Lami, was recorded as follows: peak frequency = 400.53Hz, 1st half frequency modulation = 0Hz, 2nd half frequency modulation = 0Hz, duration = 0.102s).

One infant female, Doris, produced grunts at 20 months of age. This was the only recorded case of an infant producing a grunt, and occurred when the infant was not weaned but nursing only occasionally. The infant and mother pair that the grunts were directed at were not directly related to Doris, though genetic relatedness between adults in the group is unknown and thus there could be some degree of relatedness. The grunts were produced in the following context:

Anecdotal extract (a)

Min 1: 1 month old infant Eto'o clings to his mother, Sadiya. Doris follows, grunts x 7, leaves (03/Apr/11, 07:13)

A randomly selected grunt from this bout (Fig. 05.13) was recorded as follows: peak frequency = 7430.25Hz, 1st half frequency modulation = 39.94Hz, 2nd half frequency modulation = 319.54Hz, duration = 0.01s. Thus, infant grunts are higher pitched than adult grunts, and of shorter duration. Adult grunts have a range of harmonics at higher frequencies that are absent in infant grunts (cf. Fig. 05.12) However, at a frequency range of 0-1500Hz (Fig. 05.13) it is clear that many acoustic features of the call are similar.

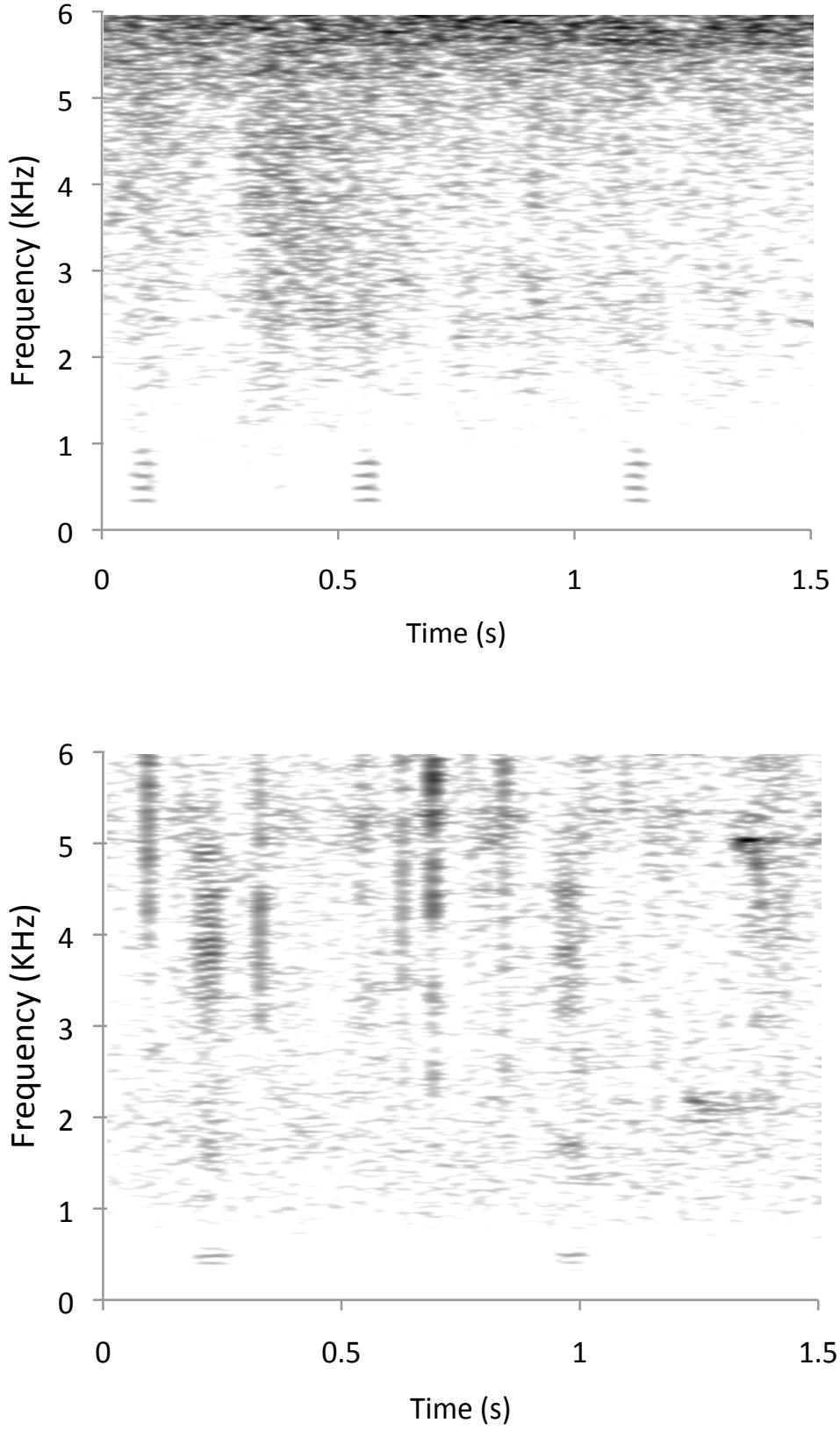

Fig. 05.12. Spectrograms of infant (top) and adult (bottom) female grunts, displayed at a frequency range of 0-6000Hz for comparison to other calls.

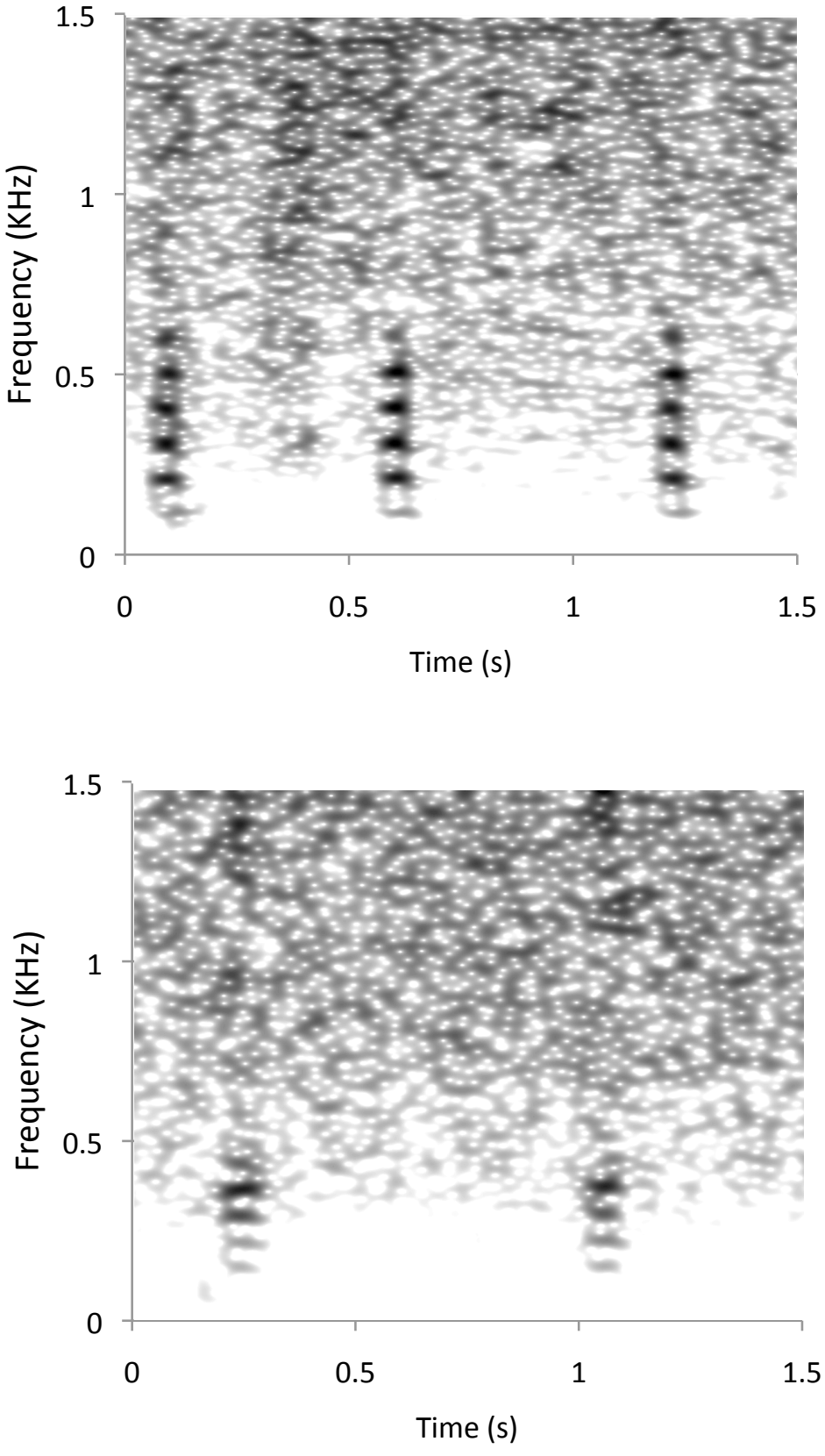

Fig. 05.13. Spectrograms of infant (top) and adult (bottom) female grunts, displayed at a frequency range of 0-1500Hz,

Pants

Adult submissive pants are glottal sounds, often produced after an aggressive encounter, or when a submissive individual is approaching a dominant group member. They are very short in duration, and atonal (Fig. 05.14). From the example, produced by adult female Rabi, a randomly selected pant from was recorded as: peak frequency = 2237.85Hz, 1st half frequency modulation = 1637.61Hz, 2nd half frequency modulation = -1477.84Hz, duration = 0.09s.

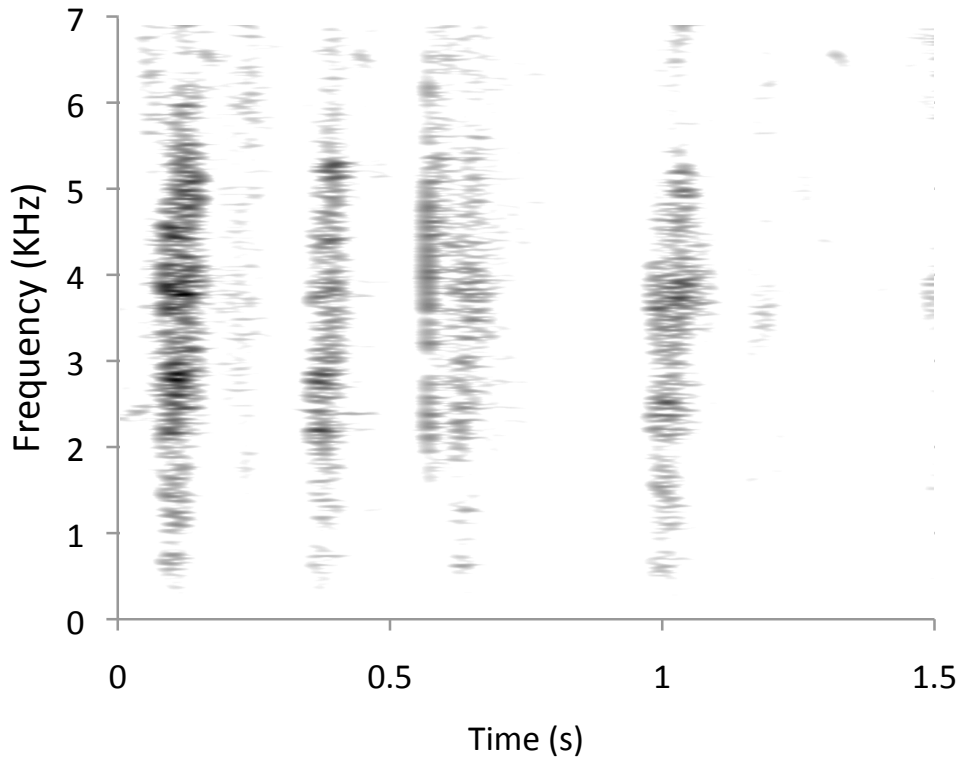

Fig. 05.14. Representative spectrogram of an adult female submissive pants, shown with a frequency range of 0-7000Hz. This shows a more atonal structure than the infant geck (cf. Fig. 05.07).

Permuted Discriminant Function Analyses

Several issues arose when applying pDFA analyses to the current dataset. In terms of classifying call types, it was only possible to run pDFAs for two individuals, Dimi (male) and Doris (female) as only these individuals contributed a minimum of three calls of each call type. These revealed mixed results, with the acoustic variables accounting for a significant amount of variation in the calls of one individual (Doris: $p = 0.030$, 94% correctly classified) but not the other (Dimi: $p = 0.134$, 49% correctly classified). Thus, the classification of call types is inconclusive, with only two of seven individuals contributing sufficient data to run such tests, and mixed results. In the case of Dimi, the number of wa-hoos produced was low in comparison to other call types, whereas Doris contributed more wa-hoos than other calls (Doris: 5 moos, 5 gecks, 11 wa-hoos; Dimi: 8 moos, 6 gecks, 3 wa-hoos).

It was possible to test for sex differences in wa-hoos and gecks, but not moos. As per conventional DFAs, cross-validated nested pDFA tests were not significant (wa-hoo: $p = 0.186$, 58.50% correctly classified; geck: $p = 0.398$, 52.91% correctly classified).

Tests for individual differences were also not significant for wa-hoos or gecks (wa-hoo: $p = 0.205$, 50.61% correctly classified; geck: $p = 0.459$, 51.90% correctly classified). In the case of gecks, the non-significant pDFA differed from the significant DFA, therefore the significant result of the DFA was due to an inflated N. Again, it was not possible to test for the effect of individual differences for moo calls (for possible explanations, see discussion).

DISCUSSION

Vocalisations produced by infant baboons are of four distinct types, and the three for which acoustic features are consistent are easily classified using those features according to regular discriminant function analyses, but using permuted discriminant function analyses, acoustic variables accounted for variation in the calls of one of two individuals. Gecks, moos and wa-hoos are easy to classify by ear, and appear to be very different upon visual inspection of spectrograms. However unfortunately, even had the results of permuted discriminant function analyses of both individuals been significant, it would not be possible to generalise such results from a sample of two individuals. It is only possible to state that the results of classification of call type are inconclusive. Thus, it is important to note that for subsequent analyses of context (chapter 6) all calls included are classified by ear.

The fact that both types of discriminant function analyses produced low rates of correct classification by sex or individual identity within call types, suggests that all infants in the group who produced three or more of any particular call type, produced wa-hoos, gecks and moos of a similar frequency, duration and frequency modulation. Different call types show different levels of pitch and tonality, as predicted by the MS rules, and will be revisited when discussing call type and context (chapter 6).

It is expected that moos and gecks will prove the most interesting of these vocalisations from an infant socialisation perspective, as they are unique to infants. In the only other study to assess behaviour associated with infant baboon vocalisations to date (Wallez and Vauclair 2012) the same two

vocalisations were identified as important in a captive setting. However, the lack of inclusion of the wa-hoo call in this previous study likely reflects the age cut off of one year, rather than its complete absence in the captive group. Furthermore, this study assumes an order of the occurrence of vocalisations according to age that was not observed in the current study – i.e. mooing was considered to predate gecking, which was not the case in the Kwano group. Further analysis of the context in which vocalisations are produced will elucidate whether this is an artefact of captivity, e.g. if a call is associated with being isolated, it is unlikely to occur in captivity but may be common in the wild.

Sex and Individual Differences

Following the theory that vocal tract anatomy determines the pitch of vocalisations to some extent (Marler 1977, Hixson 1974, Fitch 2000) one might expect to find sex differences in the vocalisations of adult baboons, where sexual dimorphism is high, and this is indeed the case in adult baboons at Kwano (Ey et al. 2007). However, this effect was slight or not present at all in infants. Male and female infants are of a similar size throughout infancy, so this effect may not be found at all. Additionally, since the two eldest infants in this group were female, their age and corresponding gain in body size compared to their younger peers might cancel out any potential sex differences.

There were some slight individual differences in gecks, but these were cancelled out when a more robust statistical test was applied. Unfortunately, it was not possible to use the pDFA method for all analyses. Having consulted a

statistics expert, it seems likely that the reason for the errors that occur when applying the nested pDFA script to the current dataset are as follows: “the problem arises from the combination of two facts: 1) [the] fourth variable (2nd half mod) basically is a constant in moos and 2) two individuals only contribute one moo call each.” (Christof Neumann, pers. Comm. 10.02.2014). After removing the two individuals who contributed only one call (analyses presented do not include these individuals) the pDFA method still produced errors. Therefore, while acknowledging that DFAs may not be the most robust statistical test due to pseudo-replication of data used in DFAs, it is not possible to apply this method of analyses to all of the current dataset.

Encouragingly, of the tests that were successful, pDFAs mainly supported the findings of the standard DFAs. As previously mentioned, in the case of call type analyses the small sample size and inconsistent results preclude any solid conclusions regarding discriminability. In the case of gecks, where a significant result became non significant when permuted analyses were used, this is not surprising since inflation of N was greater in this sample than the sample of wa-hoo calls, i.e. all individuals were sampled many times. The inflation of N was also greater for moo calls. However, since the function of a pDFA is to ensure that significant results are not the result of pseudo-replication, and the majority of DFAs (including analyses of sex and individual differences in moo calls) did not find significant results in the current study anyway, these analyses are presented to back up initial results with more robust analyses, rather than aiming to find significant results that were not reported by regular DFAs.

Infant and Adult Vocal Repertoires

Since the data collection protocol focused on infant vocalisations rather than adult vocalisations, there were not sufficient data to calculate mean values for acoustic features of adult calls. Nevertheless, it is clear from inspection of the spectrograms that the wa-hoo calls of infants and adults show similar features, and they can be recognised as similar by ear. Only the eldest infants in the sample produced wa-hoo calls, though it is not clear whether this reflects a physical inability to produce the sound at a young age, or an absence of the contexts in which this call is produced.

Do uniquely infant calls develop into uniquely adult calls?

While moos and gecks are produced only by infants, grunts and pants are produced only by adults. Therefore, it is possible that these infant calls develop into adult calls with age.

Mooing and Grunting

Though moos do not sound like adult grunts, the call structures of the two are similar, with both comprising several low pitched harmonics. Thus, it is possible that the grunt replaces the moo in an infants' vocal repertoire as it ages. However, the unusual case of a 20 month old infant beginning to grunt pre-weaning, while also producing moos at that age, suggests some overlap. Similarly, the acoustic features of the grunt produced by an infant were closer to the mean acoustic values associated with a moo than an adult female grunt. The circumstances and sound however, clearly resembled grunting rather than mooing, with the older infant, Doris, approaching the younger black infant Eto'o in an interaction resembling infant handling attempts discussed in chapter 4. At

20 months, Doris resembled a juvenile and spent much time apart from her mother, thus potentially appearing as a threat to the mother of a one month old black infant (Fig. 05.13). It seems that this transition from peer to potentially threatening infant handler may be driven by the younger infant's mother, as a point must be reached after which that mother ceases to be interested in an older infant and will not tolerate its presence.

Representative spectrograms (Fig. 05.11) showed one clear difference in the acoustic features of grunts, in that adult grunts have many harmonics at higher frequencies, while infant grunts only had harmonics at low frequencies. Since harmonics are a product of the fundamental frequency created by vocal chord vibration, this may be linked to the differing anatomy of the vocal chords of adults and infants. It may also represent one of the subtle changes in acoustic features of adult grunts when produced in different contexts (Owren at al. 2002). Though the context of the representative adult grunt is not known, the fact that its harmonics differ from the infant grunt does not mean this is always the case – given the variation in adult grunts, this may not represent a comparison of two 'infant grunts' (Seyfarth and Cheney 2007). Overall, it seems that infant moos and adult grunts are acoustically similar, but can be produced simultaneously, so it is not the case that one is replaced by the other. Rather, the social situation may be key to developing an adult vocal repertoire and ceasing to produce calls unique to the infant repertoire.

Gecking and Panting

In adults, pants are often produced as a sign of submission after aggression (Ransom 1981), and are frequently paired with a bared teeth display that

signals the same (Flack and de Waal 2007). When producing gecks, infants sometimes adopt a similar pose, though there is little evidence to suggest that the sound is associated with submissiveness in infants; moreover, it seems to be produced from a very early age to attract the attention of the infant's mother (chapter 6). Much like moos and grunts, to hypothesise that the geck might develop into the pant is not to say that they have the same meaning, rather that the sound produced is similar. It signals some form of distress in an infant, and may have a similar function in adults, though it is most commonly used as a sign of submission.

Fig. 05.15. Photograph illustrating the appearance of Doris at the time she first produced grunts (20 months of age). Doris is at the rear of the picture, with one month old black infant Eto'o, whom she attempted to handle whilst grunting, in the foreground with his mother. (Photo: Suzanne Harvey, 2011.)

Since distinctive call types are produced by infants, and these can be easily recognised by ear, listeners should be able to decipher any information communicated within infant vocalisations. Moreover, the acoustic structure of calls is often seen as innate, with little voluntary control due to physical constraints of sound production, whereas flexible production of such calls is widespread (Fitch 2010). Therefore, the next step towards understanding communication in infant olive baboons requires an analysis of the contexts in which these vocalisations are produced.

CHAPTER 06:

CONTEXT SPECIFICITY OF BABOON VOCALISATIONS

Two unnamed black infants of the Kwano group, with their mothers, Sadiya and Murna. Photo: Samara Teixeira, 2012.

INTRODUCTION

Historically, animal communication has been thought of as 'reflexive' rather than voluntary; that is, an involuntary reflex reaction to a mental state such as pain (Skinner 1957). However, voluntary vocal production has since been demonstrated in a range of primate species including lemurs, rhesus macaques, and chimpanzees (reviewed in Fitch 2010). Perhaps the most convincing evidence of voluntary vocalisation production in primates comes from studies into audience effects. For example, female chimpanzees have been observed to use copulation calls flexibly by calling more while mating with a high ranking male, but suppressing such calls if high ranking females are nearby, preventing competition from other females (Townsend et al. 2008). Additionally, chimpanzee alarm calls have been shown to exhibit the key criteria for intentionality usually only attributed to gestural communication, i.e. they were socially directed, associated with visual monitoring of the audience, and goal directed (Schel et al. 2013). Having established that primates have some level of control over the production of vocalisations, research has since focussed on the function of such voluntary calls.

Functionally referential signals

When considering whether vocalisations have any degree of 'meaning', the concept of functionally referential signalling has been dominant in field studies of primate communication for some time, though not without controversy (e.g. Seyfarth and Cheney 2003, 2010). Crucially, two criteria must be met in order to classify a call as functionally referential. Firstly, the call must be context specific - using the example of an alarm call, the referent is the predator, such

as a snake, and therefore the alarm call is produced in the context of a snake being present. Secondly, upon hearing a functionally referential call, the receiver must react in the absence of the referent, with evidence here coming from playback studies. In the first evidence of functionally referent calls, vervet monkeys (*Chlorocebus pygerythrus)* were found to produce specific alarm calls in response to different predators, such as leopards, eagles and snakes (Struhsaker 1967). When those calls were recorded and played back, they elicited context specific actions, such as adopting a bipedal stance and scanning the ground in response to a 'snake' alarm call (Seyfarth et al. 1980). The same study also showed that infant monkeys gradually develop the correct response to alarm calls, from a general arboreal vs. terrestrial distinction to a specific understanding of leopard vs. eagle alerts. Thus, vervet monkey infants begin with some innate vocal communication ability that improves with age.

In addition to the classic examples of alarm calls, food calls have been identified as functionally referential in three species (e.g. chimpanzees: Slocombe and Zuberbühler 2006; bonobos: Clay and Zuberbühler 2005, 2011; rhesus macaques: Hauser 1998). In bonobos, calls seem to reflect food quality rather than a specific food type (Clay and Zuberbuehler 2011). In chimpanzees, 'rough grunts' are given in response to food. When presented with a range of foods of differing preference, chimpanzees produce rough grunts with acoustics that vary subtly, but consistently and significantly. However, specific foods produce variation in rough grunts only within the 'highly preferred foods' category (Slocombe and Zuberbühler 2006). Therefore in chimpanzees, there is some evidence of vocalisations functioning as food

labels as well as showing variation in relation to food preference. However, this has not been replicated in the wild (Slocombe and Zuberbühler 2006). In a review of the literature on functionally referential food calls (Clay et al. 2012), the production of a call for a specific food was found to be rare, and the more common outcome of variation in calling rate depending on food quality has been interpreted as evidence that food calls most likely represent the caller's internal state. However, functional reference does not consider the underlying mechanism of call production, i.e. whether calls are produced voluntarily, or the reception of such calls. Thus, the idea of functionally referent signalling is limited in its application to language.

Communicating with a limited vocal repertoire

In species that have limited vocal repertoires, a 'one vocalisation equals one meaning' system of communication would be very restrictive. Thus far, the review of flexible use of calls has focused on calling rate and subtle variations within the same call type, such as chimpanzee pant-hoots. However, various species of primate have been shown to utilise not only individual call units, but also call combinations in order to communicate flexibly via a limited vocal repertoire (reviewed in Seyfarth and Cheney 2010). For example, Campbell's monkeys (*Cercopithecus campbelli*), who again produce specific leopard and eagle alarm calls (Zuberbühler 2001) use affixation, i.e. an additional syllable added to a call, to determine the specificity of an alarm call (Zuberbühler 2002, Ouattara et al. 2009). In this species, producing 'boom' calls before an alarm call seems to indicate a non-immediate threat, such as a falling tree, while the alarm call alone elicits responses from sympatric Diana monkeys (*C. diana*), who then produce their own corresponding leopard or eagle alarm calls

(Zuberbühler 2000). Therefore, Diana monkeys may undertand that this syntactic rule alters the meaning of the Campbell's monkey alarm call.

This however is not the only way that bouts of calls are used to communicate in primate species. Instead of simple two call combinations or affixation, putty nosed monkeys (*C. nictitans*) use long call sequences. Yet, it seems that these are not compositional in the sense that a specific order of calls can be deciphered as per human language (Arnold and Zuberbuehler 2012). Such long, complex call sequences have been referred to as idiomatic; listeners seem to understand their meaning without any compositional specificity (e.g. the English idiom "kick the bucket"; Arnold and Zuberbuehler 2012).

Semantics in Baboon Communication

The role of 'infant grunts' in infant handling events are discussed extensively elsewhere (Cheney and Seyfarth 2007; chapter 4). However, for the purposes of investigating functionally referential signals in baboons, the key point is that playback experiments have shown that individuals distinguish between infant grunts and move grunts, and produce functionally distinct responses (Owren et al. 2002). Perhaps more interesting from an infant-centred approach is that baboons extract social information from vocalisations, paying more attention to agonistic interactions when the dominant and submissive vocalisations are reversed and thus do not make sense to individuals who know the dominance hierarchy (Seyfarth and Cheney 2010). This phenomenon has also been observed in chimpanzees (Slocombe et al. 2010).

Much of the literature on adult primate communication has focused on food calling behaviour and alarm calls, which seem less important to infant

communication, as infants are reliant upon their mothers for food and protection. Therefore, while the contexts in which particular calls are produced cannot be predicted in advance, it is likely that they will be focused on social interactions rather than external stimuli such as food discovery or predator alerts. The calls that are unique to infants (gecks and moos, chapter 5) might reasonably be expected to have a role in mother-infant communication, since they are no longer produced after weaning.

Given that adult baboon vocalisations are used in specific contexts (Fischer et al. 2001, 2002), it is possible that infant vocalisatons may also do so. If so, it is also likely that context specificity will vary with age, since two vocalisations – the geck and the moo – have been identified as unique to infants (chapter 5). Thus, a transition between the infant and adult vocal repertoires must take place at some stage of development.

Infant baboons at Kwano have a limited vocal repertoire of just four distinct calls (‘moo’, ‘geck’, ‘scream’, ‘wa-hoo’; chapter 5). But, are these calls produced in specific contexts? While there have been references to the type of calls produced by infant olive baboons in the literature (e.g. guinea baboons; Byrne 1981) none have assessed whether such vocalisations are context specific. In light of the evidence reviewed here, it seems that various primate species communicate using single call units, affixation, call combinations and long call sequences. Therefore in order to investigate the context specificity in infant baboons, data are presented context specificity of single calls, call combinations, and call sequences.

If infant baboons produce calls in specific contexts, as chimpanzees do when

presented with preferable food types, for example, then particular calls or call combinations will be associated with specific social contexts. If however there is no particular information communicated in the sequence in which calls are produced yet the sequences produced still vary, the calls may instead reflect an 'on-line readout' of the infant's current state. In this case, while meaning is still communicated within the call sequence, the communication process would be ongoing and variable depending on the infant's precise situation.

MATERIALS AND METHODS

Data Collection

During focal follows of individual infants (for detail, see chapter 2), as many vocalisations (classified by ear) as possible were noted in the form of a tally, whenever they occurred. Additionally, the vocalisations of nearby infants were recorded when possible, to maximise the amount of data recorded. Whether collected during a focal follow or ad libitum, the behaviour associated with each vocalisation or series of vocalisations was also documented, producing sequences in a narrative style.

In the additional ad libitum data, it was often not possible to determine a context since observers were not following that individual prior to the onset of a vocalisation bout. It was not always possible to determine the cause of the first vocalisation in a bout; sometimes the infant was not visible when the first vocalisation was made. In these cases, no context was recorded. Therefore, sample size is specified for each set of analyses as the detail available for each event varies.

For each event, the following information was recorded whenever it was available: infant's ID and age, all behaviour associated with vocalisations (both infant and other group members), and the number and type of calls produced. This information was divided into minute blocks, as it was recorded simultaneously with instantaneous on the minute sampling of state behaviours. Therefore, while the duration of vocalisation bouts was not timed, an approximate duration can be derived from the number of minutes in which calls were produced.

Since behaviour associated with vocalisations can be complex and varied, a narrative sequence was used, for example:

Anecdotal scenario (a)

Min 1: Eric, 6 month old infant, refused nipple by his mother, Momi, moo 1

Min 2: moo 11, geck 2, moo 6, pulls nipple

Min 3: moo 1, geck 3, moo 3, moo 2, geck 1, moo 1, moves away

Min 4: moo 5, geck 4, moo 10, mother leaves, ride, moo 7

Min 5: moo 2, scream, moo 5

Min 6: moo 4

Min 7: Eric scream, cling

Min 8: Eric scream, cling

Min 9: Eric nipple contact

(05/Apr/11, 10:11)

Defining Context

The categories of vocalisation context were determined post hoc, with no predefined categories, as no previous information was available besides the fact that it could be reasonably expected that tantrums occur around the time of weaning. In fact, vocalisations occurred in various contexts throughout infancy. Context was therefore categorised using the specific behaviours recorded during vocalisation bouts.

Vocalisation bouts were associated with seven distinguishable contexts:

- 'Alone', when infants were completely alone, with no other group members nearby.
- 'Infant handling', when an adult other than the mother made contact with the infant.
- 'Refused nipple', when the mother actively rejected the infant's attempts to nurse.
- 'Without mother', when the infant was with other group members but not its mother.
- 'Carried', when the infant was clinging ventrally to its mother or riding dorsally.
- 'Aggression', when an individual other than the mother was aggressive towards the infant (e.g. bite, chase, slap).

‘Alone’ and ‘without mother’ are distinguished because call bouts sometimes occurred when other individuals were present. Yet, anecdotal evidence from field assistants suggests that the moo call functions to call an infant’s mother (Halidu Ilyasu and Maigari Ahmadu, pers. comm.).

In the field, contexts were recorded when there was a clear trigger for vocalisation behaviour, such as ‘refused nipple’ or ‘aggression’, as these were noticeable cases of an infant being silent and then beginning to vocalise. The contexts ‘alone’ and ‘without mother’ were defined by having no obvious trigger such as these, and often occurred when infants were simply resting, locomoting or feeding independently and then began to vocalise. In these cases, whether or not the infant’s mother was out of sight was noted. To be classed as ‘without mother’, the mother had to be out of sight when vocalisations began. To be classed as ‘alone’, all other individuals must be out of sight. Observations were stopped if a further social situation arose that did not match the initial context, for example if an infant was refused nipple and then a juvenile approached and chased that infant, the ‘refused nipple’ sequence was ended. However if an infant was slapped by its mother while she was refusing to allow it to nurse, this was classed as within the ‘refused nipple’ category. Since all behaviours of interest were recorded in narrative form, when assigning context categories post hoc, it was easy to determine when contexts changed in this way.

Analyses

Unfortunately, due to the nature of the dataset, inferential statistics could not

be used to test the hypothesis that individual call units or call combinations were context specific. Attempts to analyse the data using a logistic regression model with individual entered as a random factor yielded unreliable results, with extremely high standard errors. This is due to the fact that seven individuals contributed to a dataset with six context categories, resulting in 133 data points (each equalling one vocalisation bout for which there was a clearly observable context). Furthermore, the distribution across contexts was uneven, and the 'alone' and 'without mother' contexts occurred rarely, yielding few data points.

Therefore, descriptive statistics are presented, showing the patterns of vocalisation production at three levels: (a) context specificity of individual call units, (b) context specificity of call combinations (whether or not a call type is produced), and (c) call sequences (the type, number and order of calls produced).

Since the combination of all occurrence and ad libitum sampling of infant vocalisations produced a dataset of call tallies in minute blocks, the first objective of call pattern analyses was to define what constitutes a calling bout, and what should be classed as an isolated vocalisation. For example, one could interpret a series of 6 calls within a minute, followed by 2 min of silence, then 6 more calls, as either 1 or 2 call bouts. Therefore, a log survivorship analysis (Bateson 1963) is necessary. This type of analysis produces a Bout Criterion Interval (BCI), which determines whether gaps between calls represent within-bout or between-bout intervals. Thus, such a calculation determines how long an infant must be silent after a vocalisation before the next call is classified as a separate bout, as opposed to a continuation. The

objective is to determine a meaningful break point on a log survivorship plot on which to base subsequent call pattern analyses. Only after the BCI is established can one go on to consider factors such as the number of calls in a bout, and the role of call types within each bout.

RESULTS

Call Bouts

A total of 1188 bout intervals were recorded, with lengths ranging from 1-227 min. Intervals of 1 min were the most frequently observed, with 158 instances, and the general trend shows that as intervals increase, frequencies decrease. The frequencies of intervals less than 10 min in length fluctuate, and can increase or decrease; for example, more 6 min intervals were observed than 5 min intervals, contrary to the overall trend. While the frequencies of intervals greater than 10 minutes also fluctuate, this is the first point at which all subsequent frequencies are lower. Therefore, the BCI is defined as 10 min (Fig. 06.02). This affects approximately half of the intervals, with 607 intervals classified as within bout, and 579 classified as not within bout.

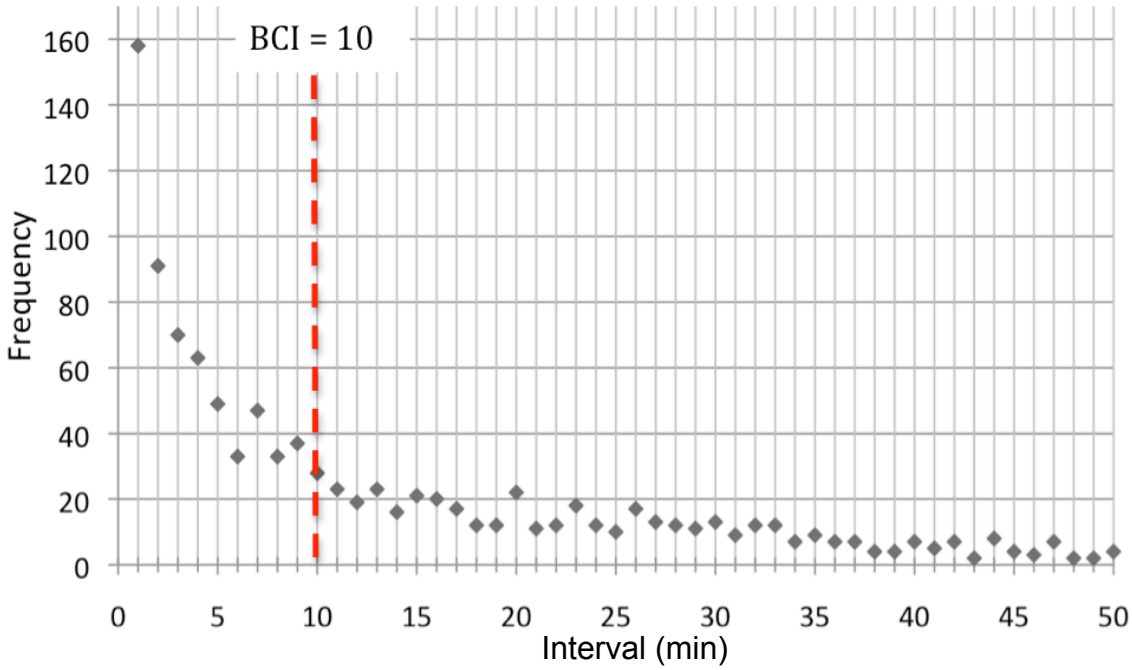

Fig. 06.01. Determining a Bout Criterion Interval (BCI) via frequency of intervals between individual vocalisations (N = 1188). After 10 min, with a frequency of 28 cases, fluctuations in frequency do not exceed this level. Therefore, the BCI is defined as 10 min. Intervals of up to 50 min are displayed for clarity, though the actual range of intervals was 1-207 min.

Context Specificity of Individual Calls

Having established what constitutes a call bout, it is now possible to assign a context to calls produced within these bouts. Before investigating the complex call sequences produced by infant baboons, it is first necessary to look at the occurrence of individual call units. Using the four call types distinguishable by ear: geck (G), scream (S), moo (M) and wa-hoo (W; definitions chapter 5) calls were classified according to the context in which they were produced. All calls were treated as single units regardless of their position in a call bout (Tab. 06.01).

Tab. 06.01. Context-specificity of different calls (N = 3565) produced by 7 infant baboons in response to social events. The number of calls produced in each context are shown for all individuals.

		Call type				
	Events (N)	Scream	Geck	Moo	Contact	
Aggression	20	96	57	70	0	223
Alone	17	30	38	190	103	361
Carried	26	61	170	328	0	559
Without Mother	13	41	107	228	33	409
Infant Handling	19	13	13	6	0	32
Refused Nipple	31	398	814	769	0	1981
	126	639	1199	1591	136	3565

General patterns in the calls produced in different contexts are clear, such as more calls being produced in response to being refused nipple than any other social trigger (Fig. 06.01), and large numbers of screams being produced in response to aggression (Tab. 06.01, Fig. 06.01). However, as the visualisations illustrate, there is a high level of flexibility in call production, with all calls except wa-hoos being produced in all social contexts (Fig. 06.02).

Data were then recoded into binary yes/no categories indicating whether or not a type of vocalisation was produced in response to each social context, production of all four call types varied, which revealed some patterns in the distribution of calls across social contexts, despite all calls except wa-hoos occurring in all contexts. Screams were always produced during aggression (yes = 20, no = 0) while gecks were always produced when refused nipple contact (yes = 31, no = 0). Moos were likely to be produced when alone (yes = 27, no = 3), being carried (yes = 19, no = 7), and when refused nipple (yes =

27, no = 4). They were less likely to be produced during aggression (yes = 6, no = 14) or infant handling (yes = 5, no = 14) and were never produced after losing nipple contact (yes = 0, no = 7). Wa-hoos were only produced in the alone or without mother contexts (yes = 11, no = 0). For example:

Anecdotal scenario (b)

Min 1: infant Dimi, 15 months old, is alone. Wa-hoo 2

Min 2: moo 2, wa-hoo 3, rec 1

Min 3: wa-hoo 1, moo 2

Min 4: wa-hoo 1

Min 5: moo 1, wa-hoo 1

Min 6: moo 3, wa-hoo 2, moo 1

Min 7: moo 2, wa-hoo 1, moo 1

Min 8: wa-hoo 1, moo, wa-hoo 3, moo, wa-hoo, moo

Min 9: juvenile female Tala approaches, embraces Dimi, rest social

Min 10: rest social

Min 11: Tala leaves

Min 12: moo 1, Tala approaches, Dimi mounts Tala, Tala leaves

Min 13: wa-hoo 1, moo 1, wa-hoo 2

Min 14: Tala approaches, grooms Dimi, leaves, Dimi wa-hoo 3

Min 15: moo 2, wa-hoo 1

Min 16: wa-hoo 3

Min 17: moo 1, Dimi approaches sub-adult Murna, rest social, feeds

Min 18: moo 3

Min 19: follows Murna, Murna grooms Dimi. (19/Jan/11, 07:28)

In the above example, the infant's mother is absent. Initially alone, he produces wa-hoo and moo calls. At times during the 19 min call bout, two other group members approach, and engage in social activity with the infant such as grooming. However, he continues to produce calls during this time. This is an example from the 'without mother' category.

All call types occurred in a range of contexts with the exception of the wa-hoo call, which occurred only when infants were alone or without their mother. Therefore, hearing these calls in isolation may have little meaning to a listener. This does not preclude the possibility that repetitions of individual call units are meaningful, but rather suggests that context cannot be inferred from a single scream, geck, or moo. Therefore, rather than assessing whether or not each call type is likely to be produced in a particular context, the next set of data show the number of each type of call produced in response to social events both per individual, (tab. 06.01) and for all individuals (Fig. 06.02). Finally, the mean average number of calls across social events for all individuals is presented (Fig. 06.03).

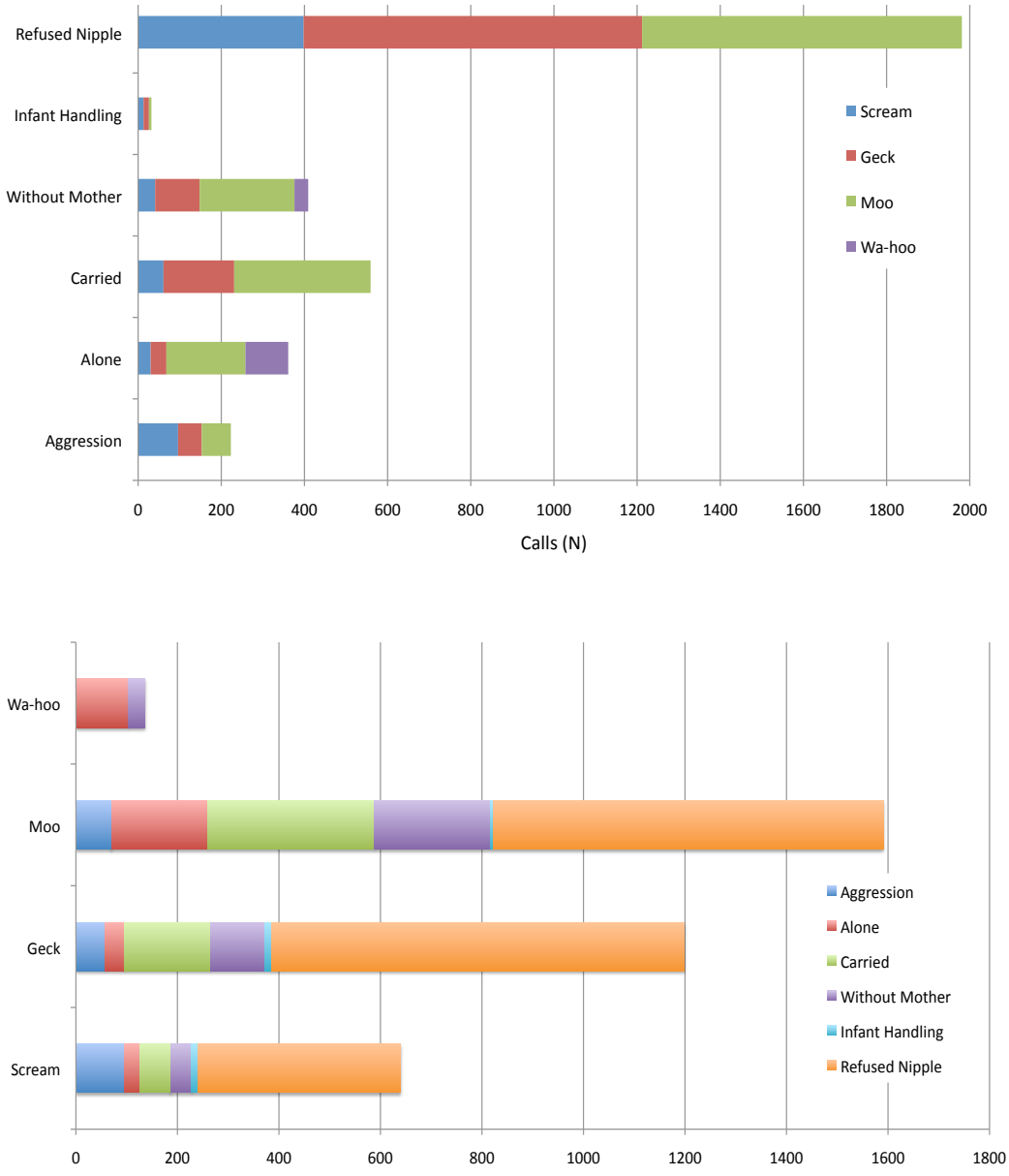

Fig. 06.02. Top: total number of calls produced in each social context, by all individuals. Bottom: total number of each call produced in each social context, by all individuals (N = 7inidividuals, 126 events, 3565 calls).

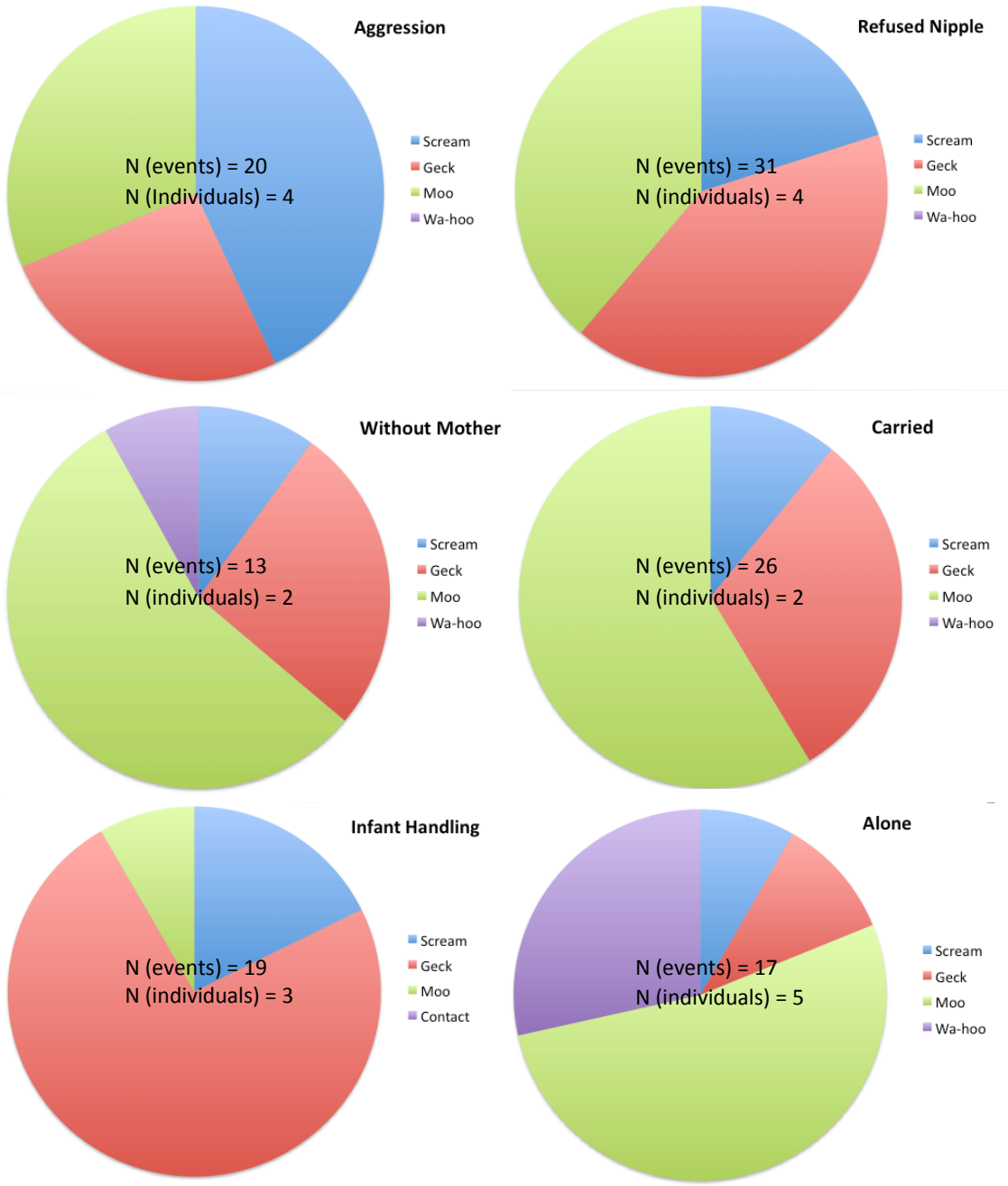

Fig. 06.03. Mean percentage of each call type produced across social contexts (N = 126 events total).

Tab. 06.02. Context-specificity of different calls produced by 7 infants in response to social events. Standard deviation calculated per individual, for all events in a given context (N = 126 events).

				Call type (mean N calls ± SD)			
Context	Infant	Sex	N	Scream	Geck	Moo	Wa-hoo
Aggression	Debbie	F	4	3.5 ± 1.0	0.5 ± 0.6	-	-
	Doris	F	6	4.0 ± 1.5	0.3 ± 0.5	-	-
	Emma	M	5	3.4 ± 1.8	0.6 ± 0.9	0.8 ± 1.8	-
	Eric	M	5	1.6 ± 0.8	1.6 ± 2.2	1.8 ± 1.8	-
Alone	Debbie	F	5	-	-	0.6 ± 0.8	3.4 ± 0.5
	Dimi	M	3	-	-	1.3 ± 0.6	3.6 ± 0.6
	Doris	F	2	-	-	4.0 ± 1.4	-
	Emma	M	2	0.5 ± 0.7	1.0 ± 1.4	3.5 ± 2.1	-
	Eric	M	5	0.8 ± 1.3	0.4 ± 0.8	2.8 ± 1.9	0.4 ± 0.8
Carried	Emma	M	10	1.8 ± 2.4	0.9 ± 1.6	1.8 ± 1.9	-
	Eric	M	16	0.9 ± 1.3	2.1 ± 1.9	1.5 ± 2.1	-
Without mother	Emma	M	6	0.7 ± 1.2	1.3 ± 2.3	3.0 ± 2.0	-
	Eric	M	3	1.3 ± 1.5	1.0 ± 2.0	2.2 ± 1.7	-
Infant handling	Emma	M	12	0.5 ± 0.5	2.3 ± 1.6	0.2 ± 0.4	-
	Eric	M	3	-	3.7 ± 0.6	0.3 ± 0.6	-
	Eggi	M	3	1.3 ± 1.5	2.0 ± 2.6	0.7 ± 1.2	-
Refused nipple	Dimi	M	6	0.3 ± 0.8	3.8 ± 1.9	0.8 ± 1.2	-
	Doris	F	4	1.5 ± 1.3	2.8 ± 1.3	0.8 ± 1.2	-
	Emma	M	10	1.1 ± 1.7	1.2 ± 1.3	2.7 ± 2.1	-
	Eric	M	10	0.6 ± 0.8	2.8 ± 2.1	1.6 ± 1.8	-

Thus far, analyses of individual call units and call combinations have shown that there is a great deal of variation within contexts, with the mean number of calls produced by each individual across social contexts often exceeded by the standard deviation of calls produced, indicating that they may or may not be produced at all.

Call Combinations

To investigate whether the type of calls produced together rather than the number of each call type contains information, each call bout was again recoded into binary yes/no categories for each vocalisation. Thus, here each letter represents the occurrence of one or more of that call type, i.e. 'S' does not represent a single scream, but a call bout in which only screams occur, while SG represents a call bout in which screams and gecks were produced (Tab. 06.03).

Tab. 06.03. Context-specificity of the different call combinations produced by infants in response to social events, for all individuals (N = 126 events).

	Context					
Combination	Aggression	Alone	Carried	Infant Handling	Without Mother	Refused Nipple
Scream	6	-	2	-		-
Geck	-	-	2	8		2
Moo	-	6	5	-	3	-
Wa-hoo	-	3	-	-		-
Scream/Geck	8	-	4	6		2
Scream/Moo	3	3	-	2	1	-
Scream/Geck/Wa-hoo	-	2	-	-		-
Geck/Moo	-	1	5	3		3
Moo/Wa-hoo	-	6	-	-	2	-
Scream/Geck/Moo	3	9	8	-	2	24

The combinations scream/wa-hoo, scream/geck/wa-hoo, geck/wa-hoo and geck/moo/wa-hoo were not produced in any of the contexts observed, The categories 'alone' and 'carried' are associated with a range of different call combinations, whereas 'refused nipple' was only associated with the combinations geck, scream/geck, geck/moo, and scream/geck/moo. In cases where scream/geck/moo combinations were produced, further antagonistic interactions were usually involved, for example:

Anecdotal scenario (c)

Min 1: Emma, 7 month old infant, refused nipple by his mother, Ymke. Moo 3, geck 15, moo 3

Min 2: geck 2, scream, moo 1, scream 3, geck 3, scream, geck 3

Min 3: moo 3, scream 10, geck, moo 2, scream, clings to Ymke, Ymke slaps Emma, scream 8, Ymke holds down Emma, Ymke leaves, Emma follows, scream 3. (20/Jan/11, 08.22)

In this example, an initial refusal to allow the infant to nurse led firstly to moos and gecks, then screams, moos and gecks in the next minute. This was then followed by aggression from the mother, prompting a further 11 screams.

Call Sequences

Calls were extracted from ad libitum data using a BCI of 10 minutes as defined above (cf. fig 06.01), and each call in the sequence was then given a number marking its position, for example (from the refused nipple context):

Anecdotal scenario (d)

Min 1: Eric, 7 month old infant, refused nipple by his mother, Momi. Geck 8, Scream, geck 3, moo 2, scream, moo 3, scream, clings to Momi's back. (16/Jan/11, 08:25)

In this example, the infant Eric was refused nipple, produced a series of calls, and then clung to his mother's back. Eric produced the following call bout, consisting of 19 calls:

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
G	G	G	G	G	G	G	G	S	G	G	G	M	M	S	M	M	M	S

Sequence data were available for 209 call bouts (only those events for which the first call in the bout could be determined), and ranged in length from 2 – 333 calls. This number exceeds the number of bouts presented in all social contexts, as call bouts with unknown social triggers were included in order to maximise the number of sequences available. These analyses aim to determine whether each call type is likely to be produced at the beginning or end of a call sequence, therefore call bouts have not been divided according to context. Longer sequences were rare, and the percentage of call types at each position in the sequence are shown up to position 42, which has a sample size of 44 call sequences (Fig. 06.04).

Moos accounted for 30% of the first calls in a sequence, while this frequency increased to 55% of the 42nd. The distribution of gecks showed a different pattern, only differing slightly between the first and 36th calls, from 23% to 27% respectively. Gecks accounted for more calls mid-sequence, for example, 47% of the 9th calls were gecks (cf. Fig. 06.04).

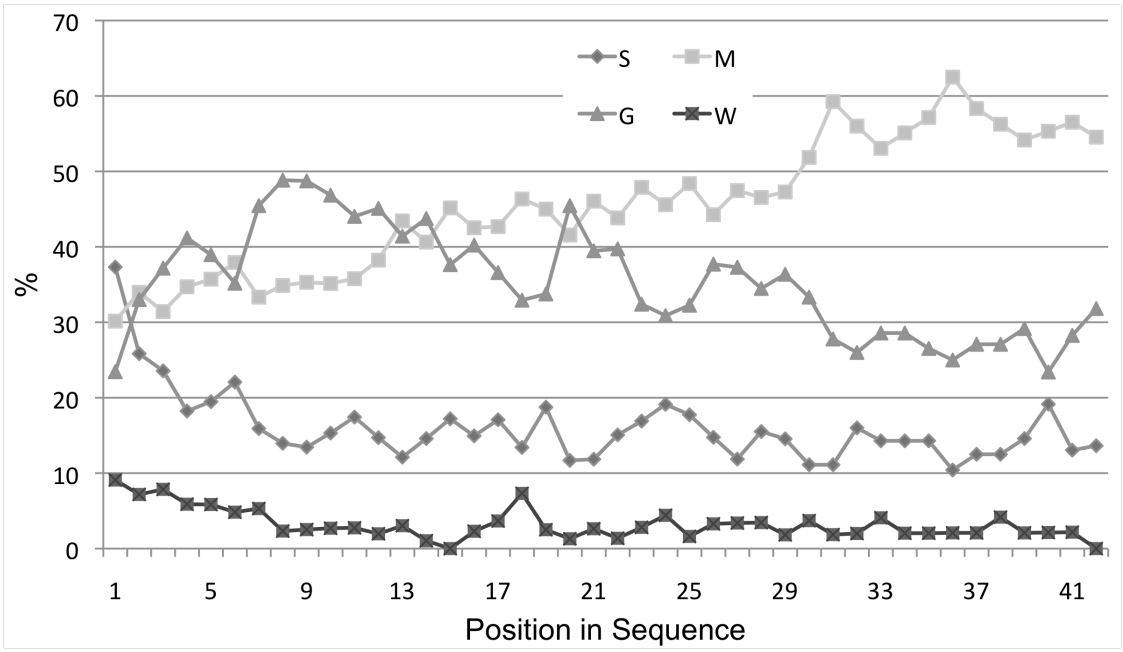

Fig. 06.04. Percentage of calls at each position in the call sequence (N = 209 call bouts).

Screams accounted for 37% of first calls, but decreased to 14% of the 42nd . Wa-hoo calls were the least common, and comprised the lowest percentage of calls at all positions in the sequence.

Call Transitions

In addition to the position of an individual call within a sequence, it is also possible to look for patterns in call transitions; the order in which pairs of calls occur. For example, in a sequence such as 'SSGM', there is one S>S, one S>G and one G>M transition. As there are a total of four call types, and each can in turn be followed by any of the four, there are 16 possible types of transition. There were a total of 6078 transitions within the 209 sequences (Tab. 06.04), of which 1042 began with a scream (S-transitions); 2218 began

with a geck (G-transitions); 2651 began with a moo (M-transitions) and 167 began with a wa-hoo call (W-transitions). The most common transitions for each type were to the same call, with 67%, 81%, 82% and 55% for S, G, M and W respectively, with the moo call most likely to follow when call type changed (tab. 06.04). Therefore, calls rarely occurred as a single unit, and mooing is the most common type of transition.

Tab. 06.04. Percentage of transition types between individual call units for (a) all call types, and (b) excluding transitions to the same call type, e.g. S>S (N = 209 call bouts).

(a)			First Call			
			Scream	Geck	Moo	Wa-hoo
		Scream	67	6	6	1
Second Call		Geck	18	81	9	2
		Moo	15	13	82	42
		Wa-hoo	0	0	2	55
(b)			First Call			
			Scream	Geck	Moo	Wa-hoo
		Scream	-	32	34	1
Second Call		Geck	55	-	52	6
		Moo	45	67	-	93
		Wa-hoo	<1	<1	14	-

DISCUSSION

Of the four calls that can be distinguished by ear in the baboon vocal repertoire (scream, geck, moo, wa-hoo; chapter 5), only one call, the wa-hoo, shows evidence of context specificity in the descriptive statistics presented. Wa-hoo calls were produced only in the contexts of 'alone' and 'without mother', and this is consistent with a previously described function of the adult wa-hoo call as a 'contact call' (Rendall at al. 2000). However in adults, these calls are also used flexibly (Fischer at al. 2001, 2002). While it is possible that wa-hoo calls are context specific in infant olive baboons, it is important to note that the 'alone' and 'without mother' contexts were associated with many different call combinations, and there was no straightforward association such as 'alone = wa-hoo calls only'.

Vocal Flexibility

Though screams, gecks and moos did not show context specificity, each of these calls appeared to have contexts in which they were more likely to be produced, while they were also produced in other contexts. For example, screams were always produced after aggression. No call type except the wa-hoo was exclusively produced in specific contexts.

Geck

Based on anecdotal evidence, it was hypothesised that mooing may function to call an infant's mother. However, gecks seem to be more targeted at an infant's mother than moos, since they are always produced in the mother-specific situations in which the infant had been rejected when trying to feed, and almost always during infant handling, when another adult tries to remove

the infant from its mother. Given that gecks are unique to infants, it is not surprising that they are produced in these infant specific contexts that would not occur after weaning. However, they also occur at least sometimes in all other contexts, thus in isolation, listeners would not be able to infer a mother-infant context from hearing a geck. Another explanation for the tendency for gecks to be produced in these particular contexts may be that they function as a relatively low level protest. Gecks often occur during infant handling, a context in which call bouts tend to be short, and handling attempts are resolved quickly since handlers rarely succeed in separating mother and infant (chapter 4). However, if infants are rejected while trying to feed, gecks were produced in combination with screams as part of a much longer and higher energy call bout.

Moo

Moos seem to be more likely to be produced later in call bouts and were the only call type that is frequently transitioned into or from all other call types. These data together suggest that mooing, which has a low peak frequency relative to other calls (chapter 5), may be used by infants as a relatively effortless way of continuing to call their mother between bouts of louder and more attention grabbing calls such as screams. An infant may want to produce nothing but high energy, attention grabbing screams when refused nipple for example, but in a call bout potentially hundreds of calls long, this simply would not be possible. Similarly in adult male baboons, where wa-hoo calls have been linked to rank and can demonstrate a male's strength and endurance, the energy in the call decreases within all bouts regardless of rank (Fischer et al. 2004). Where calls are used flexibly in the infant vocal repertoire, rather than

using a lower energy version of the same call, a relatively low energy moo call could be used instead of high-energy, high frequency gecks and screams.

While generally common across contexts, possibly as a result of their use as a transitional call and relative frequency in the latter stages of call bouts, moos were never produced after losing nipple contact. One possible reason for this is that call bouts produced in this context are characterised by their short duration, whereas moos occur in greater frequencies later on in long call bouts. Since being refused nipple prompts the most calls and longest duration of call bouts, the high proportion in which moos are produced in this context tends to favour the hypothesis that they are a low energy call used to maintain a call bout that has already consumed a lot of energy. The fact that transitions between different call types are most commonly to and from moos further supports this theory. It seems that the moo, while unique to the infant vocal repertoire, is the call most flexibly produced across all social contexts.

Wa-hoo

Following Elowson et al. (1998) as per chapter 5, wa-hoos are best considered as the only truly adult-like call that only older infants produce (chapter 5). Wa-hoo calls are also referred to as barks when produced by adult female baboons, and such barks have been shown to vary acoustically between contexts, with ‘contact’ barks being more tonal and harmonically rich (Fischer et al. 2001). This is consistent with the tonal wa-hoo calls produced by infants in the current study, and the example of a female bark recorded at Kwano (chapter 5) though adult females also produce atonal wa-hoos or barks in response to predators (Fischer et al. 2001). Age seems a key factor in the

context specificity of this call – not only does it occur only after month seven, when infants spend more time apart from their mothers (chapter 3) but the lack of flexible use of the call when it is produced by infants may again be the result of infants rarely being exposed to predators in order to produce an alarm call (Colishaw 1994).

Interestingly, in chacma baboons, infants show adult levels of understanding of the difference between female contact barks and alarm calls from six months of age (Fischer et al. 2000) and in the current study, the first wa-hoo calls were produced at seven months of age. This corresponds with a large decrease in the amount of time infants spent being carried by their mothers at seven months of age, and thus it seems likely that these calls start to be produced as soon as the 'alone' and 'without mother' social contexts occur. Some degree of understanding (the same response to alarm calls or contact calls) is shown at four months of age (Fischer et al. 2000) when most time is still spent in contact with mothers, negating the need to produce a 'contact' call (chapter 3).

Scream

Screams were always produced after aggression, and were commonly produced when an infant had been refused nipple access by its mother. It seems intuitively correct that these social contexts involving conflict should trigger a scream (reviewed in Scherer and Kappas 1988), and as a high pitched, high-energy call it may represent the highest level of emotional arousal in infants, as has been observed in adult hamadryas baboons (Rendall 2003). If screams do in fact represent heightened arousal in infants, this favours the online readout theory of communication.

Call combinations – meaningful subsets, or an on-line readout?

Overall, the data show little evidence of context specificity at the individual call level (1 of 4 calls) and no context specificity of call combinations. This, together with the fact that infant baboons in Kwano group produced very long sequences of calls with few discernible patterns, suggests that the communication process may be ongoing and variable, depending on the infant's internal state. Without the use of playback experiments, it is not possible to determine whether such long sequences are meaningful in an idiomatic way as per putty nosed monkeys (Arnold and Zuberbühler 2012), since data on the reaction of other group members would be necessary to test this hypothesis. However, with very little evidence of context specificity in individual call units or call combinations, there is no suggestion of meaningful subsets of call sequences in the current dataset.

Anecdotal scenario (c) shows an example of a sequence that suggests an online readout of the infant's internal state, with infant male Emma's mother refusing to allow him to nurse (the refused nipple context). Emma then produces gecks and moos (perhaps low level protests) followed by screams (perhaps high level protests) as he continues to be ignored. Emma's mother then slaps him and restrains him, leading to many screams. The vocalisations produced in this example may simply tell the receiver of these calls (mother or bystanders) that the infant is experiencing varying levels of distress. Therefore they may be produced after an infant is refused nipple contact or during aggression, if both produce similar states of heightened arousal. This explanation is consistent with the theory that adult male baboons use wa-hoo calls that reflect the caller's internal state, since the same call type is produced

in contexts that are very different (contests with other males in the group versus alarm calls associated with predators) but both associated with high arousal (Fischer et al. 2002). While the infant wa-hoo call closely resembles the adult female version of this call, given the sex bias in the current sample (7 male and 2 female infants) perhaps this context specificity of adult male wa-hoo calls presents a more valid comparison.

The data presented here are also consistent with the theory that vocal production in primates is constrained, as the vocal repertoire of infant baboons is limited, and three of the four calls are produced from the first week of life (Seyfarth and Cheney 1997; chapter 5). The one adult-like (Elowson et al. 1998), potentially context specific call, is used flexibly by adults during contexts that would not arise during infancy (female alarm calls: Fischer et al. 2001, male alarm calls and contest calls: Fischer et al. 2002). Ultimately, this may reflect the biological constraints of call production that limit the size of primate vocal repertoires, leading to flexible use of similar calls with subtle acoustic variations in adults (Jürgens 1995).

Future Directions

Perhaps the most stark difference between contexts is that of the 'alone' vs. 'refused nipple' contexts. While infants who are alone tend to produce wa-hoo and moo calls, often in relatively low numbers, infants who have been refused nipple tend to produce screams, gecks and moos in high numbers, seeming far more distressed. Playback experiments using these contrasting call sequences would enable one to distinguish whether other individuals in the group can infer context from hearing these call bouts despite there being no

definitive pattern or context specificity of calls, thus testing whether there is evidence of idiomatic communication in this group (Arnold and Zuberbühler 2012). Having established that other adults in the group are attracted to infants and often attempt to handle them (chapter 4) one might expect that if alerted to an infant that is alone, other group members would orient towards the sound and perhaps approach the speaker. Alternatively, if the 'refused nipple' context represents a distressed infant that is in conflict with its mother, one might predict that this would be of less interest to other group members.

SECTION IV:

DISCUSSION

CHAPTER 7

GENERAL DISCUSSION

Infant Emma climbing on his mother Ymke, with sub-adult Murna and an unidentified adult male nearby. Photograph: Suzanne Harvey, 2010.

GENERAL DISCUSSION

The overall aim of the current study was to begin investigating how baboons develop the complex social behaviour that characterises their adult behaviour. All data combined give a detailed description of infant socialisation in olive baboons living in Gashaka Gumti National Park. At 7-9 months, the greatest reduction in nursing takes place (chapter 3), the frequency of handling by other adults continues to decrease (chapter 4), and many vocalisations are produced as a result of mothers refusing to nurse infants (chapters 5 and 6). At this age, the first instances of wa-hoo calls were recorded which, together with contextual analyses, suggest that infants begin to be left alone, or in a group without their mother (chapter 6). By 19-21 months, infants nurse only occasionally (though there is individual variation), feed independently almost as often as adults, and produce wa-hoo calls far more frequently, much as adults use this call to keep in contact with the group regularly (Fischer et al. 2011).

Since the objectives (p.29) set out ways in which to investigate infants' interactions with their mothers (chapter 3) and other adults (chapter 4) as well as describing their vocal communication (chapters 5 and 6), here the findings of the current study will be discussed in terms of their relevance to the fields of infant development, and primate communication.

Infant development

While comparisons between the activity budget data presented here and activity budgets of infants at other study sites are limited due to differing data collection protocols (particularly the morning focal follows used in the current

study) this study benefits from describing infant behaviour until the complete cessation of weaning. This extends the literature on infant socialisation in these areas, since an age cut-off of 12 months is common when studying activity associated with the weaning process (Lee 1997, Nicolson 1982) and theories of infant handling have been based on data from infants 0-3 months old (market value theory; Henzi and Barett 2002).

While there had been previous descriptions of the rough handling of infant olive baboons (e.g. Packer 1980) there had been no systematic investigation of infant handling in this species until now. The hypotheses of the current study were derived mainly from studies of other baboon subspecies that have been shown to differ markedly from olive baboons in both behaviour (Henzi and Barrett 2003) and genetics (Williams-Blangero et al. 1990). For example, the market value theory of infant handling was based on chacma baboons (Henzi and Barrett 2002) while the female competition hypothesis was based on yellow baboons (Wasser and Barash 1981). Many more theories of infant handling were derived from populations where allo-mothering is common (Maestripieri 1994), and were therefore not applicable to Kwano baboons.

Correspondingly, no one of these theories was able to explain the infant handling behaviour observed in Kwano baboons. The fact that few effects of rank difference were found in infant handling behaviour is also relevant to the literature on biological markets in general, as the power differential between handlers and mothers did not seem to be as large as expected given the dominance structure of the group (Henzi and Barrett 2003). This may be related to the fact that, although Kwano is considered a marginal environment for baboons (Higham et al. 2006; chapter 2), there is a high abundance of food

available to adults all year round (Warren 2003). Therefore, there may be low levels of competition over resources despite the environment being an outlier in terms of rainfall and temperature (chapter 2).

Data are consistent with the hypothesis that the total cessation of nursing may be delayed in this study group, with occasional nursing continuing at 21 months, or 20 weeks later than another studied population (Nicolson 1982). The data presented here do not constitute evidence of a delay in the cessation of weaning, since it was only possible to compare data to this one comparable study, for which the sample size is unpublished.

However, while three of the four infants observed continued to nurse occasionally at 21 months, one older infant was also able to direct infant handling behaviour towards younger infants, and produce grunts at this age (chapter 5). While anecdotal, this observed overlap of typically infant behaviour (nursing) and typically adult behaviour (infant handling, grunting) hints at the idea that if nursing is indeed prolonged, overall social development does not suffer a corresponding delay. Rather, older infants who might be weaned already in an environment with a high availability of weaning foods (Altmann 1980) could still develop the behaviour of more mature individuals despite occasional nursing. Such findings are consistent with the inclusive fitness hypothesis, which predicts that in marginal habitats like Kwano with heavy rainfall and temperature fluctuations (chapters 2 and 3), extended investment in infants, in the form of prolonged supplementary nursing up to 21 months of age (chapter 3), will benefit both mother and infant (Hamilton 1964). While unconfirmed due to the weak nature of anecdotal evidence and lack of comparable data from other study sites, if confirmed, such observations would

also fit with the wider context of prolonged interbirth intervals at Kwano (Higham et al. 2006).

Primate communication

The findings of the current study have been discussed extensively in relation to other primate communication studies in chapter 6, and are generally consistent with the established theory that primate vocalisations are genetically 'hard-wired', and calls are produced in their complete form from the earliest instances of their production (Seyfarth and Cheney 1997). As the first documentation of the acoustic features of the infant baboon vocal repertoire, the current study also adds to the quite extensive literature on acoustic features of adult baboon vocalisations (e.g. grunts: Owren et al. 2002; barks: Fischer et al. 2001; loud calls: Fischer et al. 2000; chapters 5 and 6). Specifically, some previously undocumented acoustic similarities between uniquely infant and uniquely adult calls are highlighted (gecks and pants, chapter 5). The data suggest that infants are able to produce calls that are acoustically similar to adult calls, such as wa-hoos and eventually grunts, as they get older. Furthermore, these calls appear to be used in the correct contexts as soon as they are produced, such as 'infant grunts' and 'contact calls' (chapters 5 and 6). This does not preclude a learning phase during juvenility, since other important context specific social triggers of the wa-hoo call (predators and male competition) will only become important after infancy (Colishaw 1994).

An area of communication not discussed thus far is that of gestural communication, a mode of signalling generally thought of as far more flexible in non-human primates than vocalisations, particularly in terms of flexible

production (reviewed by Tomasello and Zuberbühler 2002). While studies are mainly based on ape gestures, it has been suggested that gestural communication takes place in social contexts that are less urgent than those in which vocalisations are produced (Tomasello and Zuberbühler 2002). Moreover in apes, playing and nursing have been associated with gestural communication (Pika et al. 2005), and therefore this mode of communication may be highly relevant to infant socialisation.

Within the gestural communication literature, 'means-ends dissociation' is key to arguments of continuity in the evolution of gestural and vocal communication. Put simply, in chimpanzees, "means-ends dissociation can be characterised by the flexible relation of signalling behaviour and goal. An individual uses for instance a single gesture for several goals (touch for nursing and riding) or different gestures for the same goal (slap ground and bodybeat for play)" (Pika and Liebel 2006, p. 268). In terms of the current findings, this is analogous to the way in which screams are elicited when refused nipple, during infant handling, while without mother, while being carried, or during aggression, while an act of aggression can elicit screams, gecks or moos (chapter 6). Because of this flexible relationship between behaviour and goal, any potential recipient of these signals must use the context in which they are produced to interpret meaning. This would necessitate a more complex process than required by a one context = one call form of communication, and one that more closely resembles the challenges of human language.

Effects of a marginal environment

As the current study provides the first description of the infant baboon vocal repertoire, the effects of a marginal environment on vocal communication are difficult to quantify. However, the production of infant specific vocalisations (gecks and moos) does not decrease until very late in infancy (19-21 months), a time when infants at other study sites are already fully weaned (Nicolson 1982), yet three of four infants continued to nurse occasionally in the current study group. If these vocalisations are indeed related to mother-infant communication and honest signals of an infant's needs (Trivers 1974), it might be expected that they will decrease in frequency if infants are weaned earlier. Without comparative studies of infant vocal repertoires at other sites, as well as comparable behavioural data to assess whether weaning is indeed delayed at Kwano, it is not possible to test this hypothesis.

Implications for Human Evolution

Ultimately, the study group were chosen due to their suitability as a model for the evolution of human communication. Kwano baboons show evidence of changes in behaviour in response to social pressures and environmental pressures. Overall, data are consistent with the hypothesis that social forces may overcome environmental ones, in that infants were able to act like adults by 20 months of age despite evidence of delayed development in terms of individuals requiring supplementary milk at 21 months of age, though these results are not conclusive. If infant-specific vocalisations such as gecks and moos have evolved as signals that communicate need to mothers, this may indeed be analogous to human infant cries (Furlow 1997). The fact that baboon infants seem to produce call sequences that are an online readout of

their emotional state is also consistent with this hypothesis (chapter 6). The decrease in infant specific vocalisations (gecks and moos) as baboons age, supports the notion that they function to provide signals to the mother, since these calls are only produced during infancy. This could be analogous to the stages of vocalisation that human infants progress through, with the two extremes of laughter and crying almost exclusively linked to happiness and distress from an early age, and 'in-between' stages of squeals and growls developing at later stages (Kimbrough et al. 1976). This study also noted that human infant sounds reflect some of the phonetic content of language developed at later ages, much as infant baboon gecks resemble adult pants (chapter 5).

Besides using baboons as a model for early hominids, another approach to studying the evolution of human cognition is that of looking for 'benchmarks'; i.e. a skill that is considerably more developed in humans than in other species. Language certainly seems to qualify as one such benchmark. However, the idea of identifying key discontinuities between human and non-human primate communication has at times been referred to as a false dichotomy (Fitch 2010) as there is much evidence to suggest that humans are unique in their ability to physically change the structure of a call (Jürgens 1995), thereby producing new sounds. In contrast, non-human primates are characterised by a small vocal repertoire and a limited ability to change vocalisation structures, though there is much evidence of subtle changes (e.g. chimpanzees: Slocombe and Zuberbühler 2006, baboons: Fischer et al. 2001, 2002, Owren et al. 2002). Therefore, while the development of infant olive baboons shows some parallels to human infant development, it is unsurprising

that the focal animals show limited vocal communication skills. The data presented here do however reflect the importance of the ecological and social environment to baboon infant development, an environment that may well be similar to that of early hominids.

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APPENDICES


THE GASHAKA PRIMATE PROJECT
GASHAKA-GUMTI NATIONAL PARK, NIGERIA & DEPARTMENT OF ANTHROPOLOGY, UNIVERSITY COLLEGE LONDON

Appendix 1. Ethogram of all data collection codes, including location, name and sex identification codes, and state and event behaviours (cont. overleaf).

BEHAVIOURAL CATEGORIES AND CODES	
AREA	
F	FOREST
S	SAVANNAH
STATES	
cl	INFANT CLINGS
nc	INFANT NIPPLE CONTACT
ri	INFANT RIDES
fe	FEEDING
gr	GROOM
lo	LOCOMOTE
pa	PLAY ALONE
ps	PLAY SOCIAL
-l	PLAY LOCOMOTE
-o	PLAY OBJECT
-r	PLAY, ROUGH
ra	REST ALONE
rs	REST SOCIAL
COMPANY	
A	ALONE
M	MOTHER
J	JUVENILE
P	PEER
c	CONTACT
n	NIPPLE CONTACT
VOC (also use in AD LIB EVENTS CATEGORY)	
va	ALARM CALL
vb	VOCAL BARK (WAHOO)
vc	VOCAL CHIRP
vg	VOCAL GRUNT
vsc	VOCAL SCREAM
vm	VOCAL MOO

Appendix 1. Cont.

AD LIB EVENTS & STATES	
bt	BARE TEETH
ch	CHASE
dp	DISPLACE
em	EMBRACE
bi	BITE
fo	FOLLOW
gr	GROOM (active/passive gr> gr<)
gb	GRAB
hd	HOLD DOWN, RESTRAIN
hs	HIT SUBSTRATE
ls	LIP SMACK
mu	MUZZLE CONTACT
le	LEAVE [MOVE AWAY - RETREAT]
pre	PRESENT
res	RESIST
sv	SHAKE VEGETATION
sl	SLAP
SCANS & BYSTANDER	
M	MALE
F	FEMALE
A	ADULT
S	SUBADULT
J	JUVENILE
I	INFANT
Ib	BLACK INFANT

Appendix 2. Data collection protocol sheet used by SH, TR and JT.

BEHAVIOURAL STUDY	DD / MMM / YY	OBSERVER	PROT. NUMBER
FOCAL ANIMAL	START:		
	END:		

SCAN NN	<2M	2-5m	>5M

	FOCAL ANIMAL ON THE DOT				AD LIB (ALL INDIVIDUALS <5M)	
	AREA	STATE	HEIGHT	COMPANY	EVENTS	BYSTANDER
1						
2						
3						
4						
5						
6						
7						
8						
9						
10						
11						
12						
13						
14						
SCAN NN			<2M		>5M	
16						
17						
18						
19						
20						
21						
22						
23						
24						
25						
26						
27						
28						
29						